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**Habitat Associations of Black-backed *Picoides arcticus* and Three-toed *P. tridactylus*
Woodpeckers in the Northeastern Boreal Forest of Alberta**

Name of author: Jeff S. Hoyt

*Title of Thesis: Habitat Associations
of Black-backed and Three-toed
Woodpeckers in the Northeastern Boreal Forest of Alberta*

Degree: Master of Science

Jeff S. Hoyt



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Thesis Advisor: Dr. David L. Smith

Other Committee Members:

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of Master of Science

Environmental Biology and Ecology

Department of Biological Sciences

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University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Habitat Associations of Black-backed Picoides arcticus and Three-toed P. tridactylus Woodpeckers in the Northeastern Boreal Forest of Alberta* submitted by *Jeff S. Hoyt* in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.

ABSTRACT

Black-backed (*Picoides arcticus*) and Three-toed woodpecker (*P. tridactylus*) numbers might decrease in boreal Alberta due to fire suppression and changes in the structure and age composition of the forest. I surveyed recently burned, old-growth and mature coniferous forests and different aged burns to determine both species' habitat associations and how long they occupy post-fire forests. I also examined Black-backed woodpecker foraging habitat selection in a 3-year-old burn. Black-backs only occupied recently burned forests, which were occupied up to 8-years post-fire. They selected moderately burned, large diameter, standing, and the lower 1/3, of jack pine for foraging. Insect data collected failed to predict Black-backed foraging habitat selection or post-fire occupancy, primarily due to sampling design problems. Three-toeds occupied recently burned, old and mature forests, but associations with mature and old forests were unclear since mature sites that were occupied had vegetation characteristics that resembled old sites. Their occupancy decreased between 3 and 8-years post-fire.

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CHAPTER 1

THESIS INTRODUCTION

1.1 Scope and rationale for the study

Woodpeckers have been recognized as an important component of forest ecosystems, creating nesting and roosting cavities for numerous other cavity-nesting birds (Anglestam and Mikusinski 1994, Steeger et al. 1996, Klenner and Huggard 1997, Martin and Eadie 1999). Their foraging sites also provide several other species with access to food resources (Miller and Nero 1983), such as Ruby-throated and Rufous Hummingbirds feeding on sap-wells created by Yellow-bellied Sapsuckers (Steeger et al. 1996). Furthermore, previous studies have also alluded to woodpeckers as possible control agents of forest insects such as wood-boring insects and bark beetles (Beal 1911, Baldwin 1968, Koplin 1972, Holmes 1990, Hutto 1995).

Information from Europe (see Anglestam and Mikusinski 1994, Martikainen et al. 1998) and northwestern United States (see Bull and Holthausen 1993, Goggans et al. 1989) indicates that traditional forest management negatively affects woodpeckers and other cavity nesting birds. These studies suggest that changes in disturbance regimes such as fire and reductions in the number of large diameter snags and amount of downed wood, diseased trees and insect infested trees, are responsible for the decreases in woodpecker numbers (Klenner and Huggard 1997).

Industrial forestry in Alberta has become a dominant feature of the boreal landscape over the past ten years (Alberta Pacific 1992, Schmiegelow and Hannon 1993). Several authors have expressed concern that a short harvest rotation period (70-90 years depending on dominant species) combined with a strong provincial forest fire suppression policy will markedly change the structure and age composition of the boreal landscape (Stelfox 1995, Cumming 1997). Black-backed and Three-toed woodpeckers are two species that may be negatively affected by these changes. Both species are thought to occupy structurally diverse old growth forests and recently burned areas (see Goggans et al. 1989, Hutto 1995, Murphy and Lehnhausen 1998), two habitat types that are likely to decrease in abundance in managed forests (Alberta Pacific 1992, Hunter 1993, Anglestam and Mikusinski 1994). Determining the habitat requirements of species

that may be sensitive to traditional forest management, such as Black-backed and Three-toed woodpeckers, and incorporating these species' needs into forest management planning and practices, will hopefully avoid repeating previous forest management and wildlife conflicts seen elsewhere.

1.2 Black-backed and Three-toed woodpecker geographical distribution and breeding biology

The Black-backed woodpecker (*Picoides arcticus*) is strictly a North American species, unlike the Three-toed woodpecker (*P. tridactylus*) which is also found in Eurasia (Boch and Boch 1974, Angelstam and Mikusinski 1994). In North America, both species are considered uncommon to rare (Boch and Boch 1974, Short 1974, Marshall 1992, Murphy and Lehnhausen 1998). Their distribution extends across the boreal forest of North America from Alaska to Newfoundland and their eastern range extends into the New England States. In Western North America the range of the Three-toed woodpecker extends south into Oregon and the Rocky Mountains, whereas the Black-backed woodpecker extends as far south as Central California and stretches east to Montana, Wyoming, South Dakota and northern New England (Boch and Boch 1974, Short 1974, Godfrey 1986, Marshall 1992).

Both Black-backed and Three-toed woodpeckers are primary cavity nesters, meaning that they excavate their own cavities, which are most often found in dead or dying conifer trees (Short 1974, Raphael and White 1984, Weinhagen 1998, Martin and Eadie 1999). Cavity excavation can begin as early as April, but the breeding season for both species is from May to July (Bent 1939, Short 1974, Steeger and Machmer 1994, Weinhagen 1998). Prior to and during cavity excavation birds are generally very active and vocal, often drumming on standing dead trees or "snags" near the nest site (Steeger et al. 1996). Both species lay between 2 and 4 eggs and incubation duties are shared by the sexes during the 10 to 14 day incubation period (Bent 1939, Steeger and Machmer 1994).

1.3 Habitat associations

Black-backed and Three-toed woodpeckers are primarily found in conifer dominated forests (Boch and Boch 1974). However, the Three-toed woodpecker is most closely associated with spruce (*Picea* spp.) and the Black-backed woodpecker, although found in spruce dominated forests, also inhabits pine (*Pinus* spp.), fir (*Abies* spp.), and

larch (*Larix* spp.) dominated forests (Boch and Boch 1974, Goggans et al. 1989, Marshall 1992).

Both species have been described as opportunistic, responding to outbreaks of wood boring insects and bark beetles in conifer forests following windfall or disease (West and Speirs 1959, Baldwin 1960, 1968, Wickman 1965, Koplin 1969, 1972, Crockett and Hansley 1978, Kroll and Fleet 1978, Bull 1980, Yunick 1985) and immediately post-fire (Bourdo and Hesterberg 1951, Blackford 1955, Mayfield 1958, Heinselman 1973, Niemi 1978, Taylor and Barmore Jr. 1980, Apfelbaum and Haney 1981, Harris 1982, Villard and Beninger 1993, Hutto 1995, Hoffman 1997, Murphy and Lehnhausen 1998, Saab and Dudley 1998). Due to the abundance of recently dead trees in these areas, wood-boring insect and bark beetle larvae, both woodpeckers' primary food source (Beal 1911, Murphy and Lehnhausen 1998), occur at higher densities than in non-disturbed equal or older aged conifer dominated forests (see Richmond and Lejeune 1945, Baldwin 1968, Werner and Post 1985, Murphy and Lehnhausen 1998).

Hutto (1995) found that in western Montana and northern Wyoming Black-backed woodpeckers appeared to be restricted in their habitat distribution to recently burned forests. Hence, long-term maintenance of Black-backed woodpecker populations may depend on a patchwork of recently burned forests (0-6 years). Murphy and Lehnhausen (1998) expanded on Hutto's prediction, adding that recently burned conifer forests likely represent source habitats (see Pulliam and Danielson 1991) for Black-backed woodpeckers; the population increases when occupying recently burned forests and decreases when occupying unburned forests. Although the Three-toed woodpecker has also been detected in recently burned coniferous forests, it has not been labeled as burn dependent (Hutto 1995, Caton 1996, Hoffman 1997, Murphy and Lehnhausen 1998). This is presumably because, although it is considered uncommon in unburned forests, it is consistently more abundant than the Black-backed woodpecker (Murphy and Lehnhausen 1998, L. Imbeau and A. Nappi personal communication). Therefore, its association with recently burned forests could be considered opportunistic more than dependent.

Previous studies that have examined the habitat associations of Black-backed and Three-toed woodpeckers in unburned forests have reported that both species primarily

occupy overmature or old growth coniferous forests (Goggans et al. 1989, Villard 1994, Steeger et al. 1996, Hoffman 1997, Weinhagen 1998). Most woodpecker species, including the Black-backed and Three-toed, require recently dead large diameter trees or "snags" for foraging and nesting (see McClelland and Frissell 1975, McClelland 1977, Evans and Conner 1979, Thomas 1979, Mannan et al. 1980, Miller and Miller 1980, Bull 1983, Raphael and White 1984, Martin and Eadie 1999, Saab and Dudley 1999). As forest stands age the number of snags increases (Tyrrell and Crow 1994, Stelfox 1995, Lee et al. 1997) and hence abundance of wood-boring insect and bark beetle larvae (Jackson 1979, Bull et al. 1986, Nilsson and Baranowski 1997), which would explain the association of Black-backed and Three-toed woodpeckers with these types of forests. However, territory size requirements of both species are poorly understood. Klenner and Huggard (1997) found Three-toed woodpecker territories' in the British Columbia interior to be as large as 1 km² and Black-backed woodpeckers in Oregon had territories equally as large as Three-toeds and larger in forest management areas (Goggans et al. 1989).

1.4 Foraging and prey base

As members of the woodpecker community, both Black-backed and Three-toed woodpeckers are largely insectivorous (Beal 1911). However, differences in foraging techniques and prey base allow them to coexist throughout most of their range (Murphy and Lehnhausen 1998). Black-backed woodpeckers feed primarily on wood-boring insect larvae (Cerambycidae and Buprestidae) which they access by drilling holes or excavating into the sapwood of the tree. Three-toeds scale and flake the bark off trees to access bark beetle larvae found directly underneath the bark (Beal 1911, Villard and Beninger 1993, Villard 1994, Murphy and Lehnhausen 1998).

Villard (1994) found that in unburned spruce dominated forests in Manitoba, Black-backed woodpeckers foraged mainly on logs and at the base of large diameter trees, whereas Three-toeds foraged higher and on smaller diameter trees. In Lodgepole pine dominated forests in Oregon, 90% and 96% of foraging observations were made on the trunk of standing trees, and dead trees were used for foraging 88% and 68% of the time by Three-toed and Black-backed woodpeckers respectively (Goggans et al. 1989). Murphy and Lehnhausen (1998), found that in a recently burned spruce dominated forest in Alaska, both Black-backed and Three-toed woodpeckers spent over 95% of their time

foraging on recently burned standing dead trees. However, Black-backs foraged primarily on moderately to heavily burned spruces where wood-boring insect larvae were most abundant and Three-toeds concentrated on the less-burnt spruces where there was an abundance of bark beetle larvae (Werner and Post 1985).

Recently burned forests represent suitable habitat for wood-boring insects and bark beetles due to the increased density of recently killed standing dead and dying timber (Parmalee 1941, Richmond and Lejeune 1945, Alberta Environmental Protection 1999). Wood-boring insects and bark beetles are attracted to forest fires both during the fire and immediately after it has passed through an area (Evans 1966, Werner and Post 1985, Ives and Wong 1988, Hart 1998). They attack the charred areas of conifer trees and deposit their eggs in crevasses in the bark (Alberta Environmental Protection 1999). The heaviest attacks occur in those trees burned during the spring (April to June) and the density of attacks decreases later in the season, because adults are only in flight during late May to July (Alberta Environmental Protection 1999). The moisture content of the wood limits wood-boring insect and bark beetle larvae occupancy of standing dead trees post-fire; as trees dry out and the moisture content decreases, larvae development and survival decreases (Werner and Post 1985).

1.5 Management of Black-backed and Three-toed woodpeckers in the boreal forest of Alberta

Black-backed and Three-toed woodpeckers have historically been two of the least studied and hence least known of North America woodpeckers (Bent 1939, Short 1974). Although, in recent years they have received more attention due to concerns that traditional forest management may negatively affect these two species (see Goggans et al. 1989, Villard 1994, Angelstam and Mikusinski 1994, Steeger et al. 1996, Hoffman 1997, Klenner and Huggard 1997, Murphy and Lehnhausen 1998, Saab and Dudley 1998, Weinhagen 1998, Martin and Eadie 1999). The results of these studies suggest that both species might decrease in abundance through habitat loss and changes in forest structure (i.e. loss of large diameter snags, downed wood, diseased trees and insect infested trees) under the proposed harvesting regimes in Alberta. However, the locations where these studies took place were highly variable with respect to dominant tree species composition

and disturbance regimes, which suggests that local studies are needed to provide recommendations for the management of these two species in the boreal forest of Alberta.

1.6 Statement of purpose

The purpose of this thesis was to determine the habitat relationships of Black-backed and Three-toed woodpeckers in the boreal forest of Alberta and based on these data, provide recommendations for maintenance and management of their habitat. The first step towards addressing how changes in the structure and age composition of the boreal forests may affect these two species, is to determine which habitat types they occupy within the boreal forest of Alberta. To do this I surveyed old growth, mature and recently burned coniferous forests for Black-backed and Three-toed woodpecker presence or absence.

In order to manage for Black-backed and Three-toed woodpeckers and the recently burned forests that they appear to be closely associated with, it is essential to determine how long post-fire forests remain suitable habitat for both species. Therefore, the second objective was to examine Black-backed and Three-toed woodpecker occupancy of different aged post-fire forests. In conjunction with this objective I conducted coarse scale insect sampling in different aged burns to determine if food availability limited post-fire occupancy. The third objective of the study was to determine the vegetation characteristics that best predicted woodpecker presence or absence in the forests that I sampled. These objectives are addressed in the second chapter of the thesis.

The first three objectives of the study are primarily descriptive, examining patterns of woodpecker occupancy. In the third chapter of the thesis I examined Black-backed woodpecker foraging, one of the mechanisms responsible for the patterns of Black-backed woodpecker occupancy observed in the 3 year post-fire forest. Therefore, the fourth objective of the study was to determine Black-backed woodpecker foraging habitat selection in a 3 year post-fire forest. I examined the characteristics of trees used for foraging and compared trees used for foraging to those available on the foraging territory. In conjunction with this objective I conducted coarse scale insect sampling in an attempt to correlate insect infestation levels with woodpecker foraging habitat selection. The fifth objective was to examine differences in foraging tree selection and foraging behavior between male and female Black-backed woodpeckers. Conclusions,

recommendations for future research and management recommendations are addressed in the fourth chapter of the thesis.

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CHAPTER TWO

HABITAT ASSOCIATIONS OF BLACK-BACKED AND THREE-TOED WOODPECKERS IN THE BOREAL FOREST OF ALBERTA.

2.1 Introduction

Black-backed (*Picoides arcticus*) and Three-toed (*P. tridactylus*) woodpeckers are residents of the boreal forest and inhabit old growth coniferous forests, burns, and other areas of standing dead trees or “snags” (Godfrey 1986, Villard 1994, Murphy and Lehnhausen 1998). Both species occupy spruce dominated forests (*Picea glauca* and *P. mariana*), but the Black-backed woodpecker is also found in pines (*Pinus spp.*) and other conifer-dominated forests (Boch and Boch 1974, Goggans et al 1989). In unburned forests both species require large diameter coniferous trees for nesting, which are found primarily in structurally diverse old growth forests (Bull 1983, Villard 1994, Hoffman 1997, Weinhagen 1998). Trees such as these may not be present within mature forests (<100 yrs) due to the lack of structural diversity (Stelfox 1995). Little is known about the habitat preferences of these woodpecker species in the Canadian boreal forest but information from elsewhere suggests that they might decrease in abundance through habitat loss under the proposed harvesting regimes in Alberta (Angelstam and Mikusinski 1994, Steeger et al. 1996, Murphy and Lehnhausen 1998, Martin and Eadie 1999).

In recent years numerous studies have alluded to the possible burn dependency of Black-backed woodpeckers, primarily that this species may require early post-fire conditions (0-6 yrs) for nesting and foraging (Hutto 1995, Murphy and Lehnhausen 1998, Saab and Dudley 1998). Although Three-toed woodpeckers have not been described as burn dependent, they are also frequently found in recently burned forests (Hutto 1995, Caton 1996, Hoffman 1997, Murphy and Lehnhasuen 1998). In recently burned forests Black-backed woodpeckers feed primarily on wood-boring insect larvae (Cerambycidae and Buprestidae) found in the sap wood of conifer trees, whereas Three-toeds feed primarily on bark beetle larvae (Scolytidae) located directly under the bark (Beal 1911, Short 1974, Murphy and Lehnhasuen 1998). Previous studies have shown that food availability and not nest site availability may be limiting occupancy of post-fire forests by both woodpecker species (Caton 1996). To better understand the population dynamics of

these two species in post-fire forests it is essential to determine how long both species occupy these forests.

The boreal forest is quickly becoming a leading frontier for forest operations in Canada. During the past ten years within Alberta, the majority of the boreal forest ($>220\ 000\ km^2$) has been committed to various forest companies (Schmiegelow and Hannon 1993). A short harvest rotation period (70-90 years depending on dominant species) combined with a strong provincial forest fire suppression policy will markedly change the structure and age composition of the boreal landscape (Stelfox 1995, Cumming 1997). Several forestry companies in Alberta have embraced the concept of ecologically sustainable forestry (or ecosystem management) (Grumbine 1994), which emphasises the retention of ecological processes and biodiversity in the forest in combination with fibre removal (Alberta Pacific 1992). One approach is to design harvesting practices to mimic fire at the stand and landscape scales (Alberta Pacific 1992, Hunter 1990, 1993, Bunnell 1995). Despite this attempt at coarse filter management for biodiversity, there will be species that are fire or old growth dependent that may “slip through the cracks.”

I examined Black-backed and Three-toed woodpecker occupancy of recently burned, mature and old growth coniferous forests in Alberta. Based on the results of my first objective, two secondary objectives were established. The first objective was to determine if distance from recently burned areas greater than 200 ha, influenced Black-backed and Three-toed woodpecker occupancy of old growth white spruce and black spruce dominated stands. The second objective was to determine Black-backed and Three-toed woodpecker occupancy of forests aged 3, 4, 8, 16 and 17 years post-fire. In conjunction with this objective I conducted coarse-scale insect sampling in the 3, 8, and 16 year post-fire forests to determine if food availability was limiting woodpecker occupancy of post-fire forests. My final objective was to determine which vegetation characteristics best predicted woodpecker presence or absence in the forests that I sampled.

2.2 Methods

2.2.1. Study area

This study was conducted in the northeastern boreal forest of Alberta during the spring and summer of 1997 and 1998 (Appendix I). Sampling in 1997 was concentrated in a recently burned forest in Mariana Lake, Alberta ($55^{\circ} 5' N$, $111^{\circ} 55' W$) and in unburned conifer dominated forests within 50 km of the fire (Appendix I). The forest burned in April of 1995 in a 135,000 ha stand-replacing fire, and hence it was 2 years post-fire in 1997 and 3 years in 1998. Prior to burning this area was dominated by black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) with smaller patches of mixed-wood forest dominated by white spruce (*Picea glauca*) and aspen (*Populus tremuloides*) (Alberta Forestry, Lands and Wildlife 1985). In 1998, sampling expanded to include the Calling Lake region (an unburned conifer dominated area approximately 150 km southwest of Mariana Lake) and two replicates each of forests aged 3, 8 and 16 years post-fire (Appendix I). In the 3 and 8-year post-fire forests, the majority of the burned trees remained standing and the regenerating forest was generally less than 1 m. In the 16 year post-fire forests fallen trees were much more prevalent and the regenerating understory generally reached between 1 and 3 m (J. Hoyt unpublished data).

2.2.2 Habitat association surveys

Habitat association surveys for Black-backed and Three-toed woodpeckers were conducted between 8-23 April 1997 and 1998 in three types of forests in the Mariana Lake region; recently burned, mature and old growth coniferous forests. I defined old white spruce and jack pine stands as more than 110 years old, corresponding to a decade of origin of 1880 or older, and mature stands as less than 110 years, corresponding to a decade of origin of 1890 or younger. Old black spruce stands were classified as 110 years or older, but only 1880 origin stands that were height class 2 or greater (12.1 – 18.0 m) were included as old and 1880 origin stands of height class 1 and 1890 origin or younger stands were classified as mature.

Within each of recently burned, mature and old growth coniferous forests 20-25 sites were sampled in each of white spruce, black spruce and jack pine dominated stands (see Figure 2.1). Sites were placed in separate forest stands with the exception of three burned white spruce and two mature jack pine sites that were placed in the same stands. I

used Phase 3 Forest Inventory maps to determine stand boundaries, ages and dominant species composition (Alberta Forestry, Lands and Wildlife 1985). Sites located in the recently burned forest were within approximately 15 km of highway 63 and spanned a 40 km length of the highway. Old and mature white spruce and black spruce sites were primarily concentrated within a region between 10 and 50 km south of the recently burned forest within 15 km of highway 63, but there were also a few sites located approximately 10 km north of the burned area. Old and mature jack pine sites were located within 15 km of highway 63 between 40 and 65 km south of the recently burned forest (Appendix 2.1).

All sites were sampled by playing a recording of a call-drumming sequence of Black-backed or Three-toed woodpeckers in each of the four cardinal directions, with a three-minute pause between species (see Steeger and Machmer 1994). Sites were sampled between dawn and 3 PM and I found no effect of time of day on response rate. I used 200 m as a conservative estimate of the broadcast radius of the playbacks in the unburned sites, since I could not hear the recording beyond 175 m. In the more open burned forest sites the volume was lowered to obtain the 200 m broadcast radius. A tree was flagged at each site and sites were separated by a minimum of 600 m and on average 800-1000 m, to ensure no overlap in broadcast radii between sites. Sites were placed a minimum of 200 m from adjacent edges or adjacent habitat types and visited once to determine the presence or absence of Black-backed or Three-toed woodpeckers. If a male, female or both sexes of a particular species were detected this was considered a positive response and recorded as a presence. If two pairs of the same species were detected at any given site this was recorded as a single presence. Due to the similarity of Black-backed and Three-toed woodpecker's drumming and calling, a visual observation and positive species identification was necessary before a positive response to the playback could be recorded.

Burned black spruce sites surveyed in 1997 were resampled in 1998 over the same time period as 1997 to test for a difference in the timing of woodpecker responses between years. Provided no year effect exists, 1997 and 1998 sampling data will be combined.

2.2.3 Black-backed and Three-toed woodpecker occupancy of old growth conifer forests in relation to distance from recently burned forests

Sampling was conducted between 8-23 April 1998 in old growth white and black spruce dominated stands at a distance of 75 km and 150 km from any recently burned (0-5 yr) areas greater than 200 ha. The 75 km sites were located 75 km due south of Mariana Lake and the 150 km sites were located in the Calling Lake region (Appendix I). At each location 20-25 sampling sites were placed in each of black spruce and white spruce dominated stands. Sites were placed in different forest stands with the exception of two old black spruce and two old white spruce sites at each of the 75 km and 150 km locations, which were placed in the same forest stand. Stand age and species composition designations followed those outlined previously and sites were surveyed once for Black-backed and Three-toed woodpecker presence using the same techniques as described above. Sampling was evenly distributed between the two locations throughout the sampling period.

2.2.4 Black-backed and Three-toed woodpecker occupancy of different aged post-fire forests

Black-backed and Three-toed woodpecker presence or absence was surveyed in post-fire forests aged 3 (Mariana Lake), 4, 8, 8 (hereafter referred to as 8a and 8b), 16, and 17 years post-fire (Appendix I). The 3 and 4 year post-fire forests represented one replicate, both 8 year post-fire forests another and the 16 and 17 year post-fire forests the final replicate. Therefore, there were a total of 6 post-fire forests roughly representing 3 post-fire age categories; 3, 8 and 16 years post-fire. Post-fire forests were selected based on the availability of fires on the landscape and also their accessibility. In each of the 6 fires, 20 to 25 sites were sampled between 3-24 April 1998 using the same techniques as described above. All sites were placed in separate forest stands dominated by burned black spruce and mixed black spruce-jack pine. Sites were placed a minimum distance of 600m apart and on average 800 to 1000 m separated sites. All fires were greater than 2000 ha (2160 to 135,072.05 ha) to allow for the sites to be placed within the fire boundary (Table 2.1). Prior to burning, all sites were black spruce dominated with pockets of black spruce-jack pine mix, white spruce and aspen (Alberta Forestry, Lands and Wildlife 1985). Black spruce habitat was chosen due to the abundance of burned

black spruce on the landscape, as well as the absence of salvage logging in these areas. For the Mariana Lake fire, the burned black spruce sites sampled in 1998 were the same as those sampled in 1997 with the addition of 5 new sites.

2.2.5 Vegetation sampling

Vegetation data were collected at all sites surveyed in 1997 and 1998. The 200m broadcast radius was broken down into three zones representing the proximate (0-67m), middle (67m-133m) and outer (133m-200m) ranges of the broadcast radius. To ensure that the vegetation sampled would be representative of the 200 m radius around the site, a total of 100m of transects was divided among the three different zones based on what percentage of the total broadcast area each zone represented. A 27.9m transect running east/west was placed 185m north and south of the flagged tree, a 16.55m transect running north/south was placed 100m east and west of the flagged tree and an 11.1m transect running northeast/southwest was placed directly through the centre point. Transect locations were consistent at all survey sites. All trees greater than 35mm diameter at breast height (DBH) within 0.5m of either side of the transect were sampled. The following vegetation variables were collected: tree species; class (representing burn and decay classes); DBH (in mm); and condition (indicating whether the tree was standing or had fallen down). Ten tree species were counted: white spruce, black spruce, aspen, jack pine, balsam poplar (*P. balsamifera*), white birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), alder (*Alnus sp*), tamarack (*Larix laricina*), and unknown species. Classifications used to describe burned trees in the 1997 and 1998 Mariana Lake habitat association surveys sites were different than those used to describe trees in the post-fire forests surveyed in 1998, because more variation in the % of bark intact was observed in older post-fire forests. The following classifications were used to describe burned trees in post-fire forests in 1998:

Burned Trees

- 1:** lightly burned trees (1-80% burn, 100% bark intact)
- 2:** moderately burned trees (100% burn, 80-100% bark intact)
- 3:** heavily burned trees (100% burn, 50-80% bark intact)
- 4:** severely burned trees (100% burn, 0-50% bark intact)
- 5:** charred snag (0% bark and wood severely burned)

6: burned stump < 50 cm

7: recently burned salvage logged stump

8: older burned snag (20-50% bark intact, wood gray and beginning to soften)

9: older burned sang (0-20% bark intact, wood gray and beginning to soften)

10: older burned snag (0% bark intact, wood gray and soft)

However, I did not distinguish between heavily burned trees (100% burn, 50-80% bark intact) and severely burned trees (100% burn, 0-50% bark intact) in the Mariana Lake burn (see section 2.2.2.). Therefore, heavily burned trees in the Mariana Lake surveys are defined as trees with 100% burn and 0-80% bark intact. Mariana Lake burned black spruce sites resampled in 1998 as part of the post-fire occupancy surveys (see section 2.2.4), were also resampled for vegetation data in 1998 using the protocol consistent with the other post-fire forests.

Classifications used to describe the state of decay and whether the tree was alive or dead, were the same at all sites in both years, and were as follows:

Dead Unburned Trees

11: unburned, recently killed and twigs and leaves intact

12: unburned, recently killed, twigs and leaves lost and wood intact

13: unburned, dead, small branches lost and bark beginning to peel

14: unburned, dead and only major branches remain, < 20% bark peeling

15: unburned, dead, canopy broken and bark condition variable

16: unburned, dead decomposing stump < 4m and > 20% bark peeling

Live Unburned Trees

17: unburned, live and < 5% dead twigs and branches

18: unburned, live and 5-80% dead twigs and branches

19: unburned, live and > 80% dead twigs and branches

2.2.6 Insect sampling

Insect sampling was conducted between 15-25 July 1998 in the 3, 16 and one of the 8 year post-fire forests (8b). A total of 32 trees were sampled from each burn: 16 black spruce and 16 jack pine. Trees selected were between 110 mm and 200 mm DBH, roughly coinciding with the 95% confidence intervals for the DBH of trees used for foraging by Black-backed woodpeckers (see chapter 3). The 16 trees of each species

were selected to represent the 3 most abundant burn classes of trees in each burn: 3-year, Burn class 1, 2 and 3; 8-year, Burn Class 2, 3 and 4; and 16-year, Burn Class 8, 9 and 10. For each tree a total of 3, 30 cm sections were obtained. Sections were cut from the base of the tree (approximately 10-20 cm off the ground), the middle and the top of the tree (approximately 30 cm from the tip). The sections were placed in plastic bags and stored in a refrigerator at 5 °C until March 1999. Upon removal, each section was cut into 10 one-inch thick slices using a bandsaw. I chose this technique as opposed to rearing the larvae in emergence cages (see Langor 1988, Weslien and Schroeder 1999) due to the space required for cages and the time frame for emergence (1 to 3 years depending on the species) (Raske 1973, Werner and Post 1985, Ives and Wong 1988, Alberta Environmental Protection 1999).

Slices were examined for wood-boring insect larvae (Cerambycidae and Buprestidae) and bark beetle larvae (Scolytidae). For each 30 cm section, the bark was removed from each of the 10 slices and bark beetles were collected and wood-boring insects were also removed from the galleries in the sapwood of each slice. Bark beetle larvae concentrate directly under the bark near the phloem whereas wood-boring larvae bore into the sapwood to various depths, depending on species (Ives and Wong 1988). Therefore, I considered all insect larvae located directly under the bark to be bark beetle larvae and all insect larvae within the sapwood of the tree to be wood-boring insect larvae. All insects were placed in 80% ethanol until they were removed and dried at 50°C for 24 h (after Zach and Falls 1979) and weighed to obtain a separate biomass for bark beetles and wood-boring insects for the base, middle and top of each tree. All measurements were calculated for each of the three burn ages separately. Ants and spiders were not included in biomass calculations, as they have not been documented as primary food items for Black-backed woodpeckers (Beal 1911).

2.2.7 Analyses

2.2.7.1 *Black-backed and Three-toed woodpecker habitat occupancy*

I used a Kolmogorov Smirnov test to examine the effect of year on response rate of Black-backed and Three-toed woodpeckers in burned black spruce sites sampled in 1997 and 1998. Randomized G-tests were used to examine differences in Black-backed and Three-toed woodpecker occupancy of recently burned, old growth and mature

coniferous sites and different aged post-fire forests. When a significant G-statistic was observed I used a simultaneous test procedure to test for differences between groups. All randomized G-tests, were calculated based on 10, 000 randomizations. I set alpha to 0.10 because of the small sample sizes and low power to detect differences (Cohen 1988). For the Kolmogorov Smirnov test I set alpha to 0.05 because this test is relatively robust to small sample sizes (Siegel 1956).

My intention was to first examine the effect of habitat on woodpecker occupancy using age classifications from Phase 3 Forest Inventory data that would be available to forest managers. However, I suspected that several sites that were classified as mature from Phase 3 data had vegetation characteristics that resembled more closely old sites than mature sites and *vice versa* for old sites. Therefore, I performed a discriminant function analysis (DFA) to determine if vegetation data collected at old and mature white spruce and jack pine sites, classified sites differently than Phase 3 Forests Inventory data. I then performed a subsequent randomized G-test with the revised old and mature classifications.

I also used a DFA to determine if old growth white and black spruce sites located 75 km and 150 km from recently burned areas differed in vegetation characteristics. Provided that there were no differences in vegetation characteristics between the two locations, the effects of distance from recently burned forests and vegetation on woodpecker occupancy of old growth white and black spruce sites would be examined with a randomized G-test and logistic regression models respectively. However, if differences in vegetation existed between the 75 km and 150 km sites, a randomized G-test would not be appropriate to test the effect of distance on woodpecker habitat occupancy since this would be confounded by differences in vegetation between the two locations. In this case the effects of distance and vegetation on woodpecker occupancy would be examined in a single logistic regression model for 75 km and 150 km black and white spruce sites respectively (Table 2.3).

Discriminant function analysis calculates linear combinations of independent, or predictor, variables and uses these to classify cases, in my case sites, into the proposed groups; mature or old, and 75 km or 150 km (SPSS Inc. 1994). Predictor variables used in the respective analyses are outlined in Table 2.2. Prior to performing the discriminant

function analyses the normality of all variables was examined using a Kolmogorov-Smirnov goodness of fit test (Zar 1996). All variables in all analyses were normally distributed with the exception of the analysis of 75 km and 150 km old white spruce sites, where variables were log transformed to meet the assumptions of normality. I used the enter method for variable selection in all analyses and I used the Wilk's Lambda statistic to determine the significance of the model. The One-way ANOVA option in SPSS was used to test for the equality of group means for each variable. Due to the small sample size and high variability within the data, I chose an alpha level of 0.10 (Cohen 1988).

2.2.7.2 The effect of vegetation on Black-backed and Three-toed woodpecker presence or absence

Logistic regression models (Hosmer and Lemeshow 1989) were used to determine which vegetation variables best predicted Black-backed and Three-toed woodpecker presence or absence in recently burned forests, different aged post-fire fire forests, mature and old growth coniferous forests, and 75 km and 150 km sites. The binary dependent variable, occupancy, was coded as 1 = presence, 0 = absence. The independent variables used in each of the respective analyses are outlined in Table 2.3.

Prior to running the logistic regression models I preformed a Spearman's rho bivariate correlation of all variables in each of the respective models to reduce the chances of collinearity (Menard 1995). When variables were highly correlated ($r > 0.70$) I ran simultaneous models, with correlated variables in different models. In all analyses I used a classification cut-off of 0.5. I used a forward conditional method for entry of variables into the model for all analyses and 0.10 as the probability for variable entry and removal from the model, since 0.05 is considered too low and often excludes important variables from the model (Menard 1995). When no variables entered the model at 0.10, I increased the probability for entry into the model to 0.15, as an exploratory measure. I did not examine interactions in any analyses because; 1) interaction terms were often correlated with other variables in the model and 2) the large number of interactions would have increased the number of variables in the models beyond the preferred limit of 20 (Menard 1995).

I present results for only the final model, which was selected based on which of the simultaneous models best predicted woodpecker presence as determined by the

classification tables. Classification tables compare the predicted number of presences and absences to the observed outcomes based on the variables in the model (SPSS Inc. 1994). Since my objective was to determine which vegetation characteristics best predicted woodpecker presence, I was most interested in how many observed presences the model correctly classified. In addition to the classification table values I report the Nagelkerke R² and the model Chi-Square for the final model. The Nagelkerke R² is comparable to the R² obtained from a linear regression and can be defined as the proportion of variance in the dependent variable explained by the regression model (Nagelkerke 1991). The model Chi-Square tests the null hypothesis that except for the constant, the coefficients for all of the variables in the final model are equal to 0, which is comparable to the overall F test for a regression (SPSS Inc. 1994). To test for the significance of the model Chi-Square I used an alpha level of 0.10 in all analyses.

2.2.7.3 *Insect data*

A Kolmogorov Smirnov goodness of fit test was used to examine the normality of bark beetle, wood-boring insect and total insect biomass variables (Zar 1996). Kruskal-Wallis tests were used to examine differences in bark beetle biomass, wood-boring insect biomass and total insect biomass (bark beetle and wood-borers combined) between different aged burns. Following a significant Kruskal-Wallis test, nonparametric Tukey multiple comparison tests were used to test for differences between burn ages (Zar 1996). In all analyses of insect data I used an α -level of 0.10 to decrease the chance of committing a Type II error (Cohen 1988).

All DFA, logistic regression analyses and Kruskal-Wallis tests were performed using SPSS (version 8.0).

2.3 Results

2.3.1 *Habitat association surveys*

There was no difference in timing of responses between 1997 and 1998 for either Black-backed or Three-toed woodpeckers ($Z=0.275$, $p = 1.00$, and $Z=0.128$, $p = 1.00$ respectively), therefore in all subsequent analyses 1997 and 1998 habitat association data were combined.

2.3.1.1 Three-toed woodpeckers

Three-toed woodpeckers were detected in burned, old and mature coniferous forests, based on stand ages obtained from Phase 3 Forest Inventory Maps. Within all three forest types they occupied white spruce, black spruce and jack pine habitats similarly ($G=2.92$, $p = 0.261$, $G=0.830$, $p = 0.703$ and $G=1.596$, $p = 0.762$ respectively, Figure 2.1). Occurrence was similar in burned sites, old growth sites and mature white spruce and jack pine sites ($G=10.39$, $p = 0.244$), but occurrence was significantly less in mature black spruce sites than other sites ($G=16.21$ $p = 0.07$, Figure 2.1).

Mature and old white spruce and jack pine sites differed significantly in vegetation characteristics (Wilk's Lambda = 0.451, $p < 0.001$ and Wilk's Lambda = 0.250, $p < 0.001$, respectively) and the DFA classified old and mature sites differently based on vegetation characteristics than Phase 3 Forest Inventory data. Sites classified as old white spruce had a lower density of deciduous and standing trees and a higher density of downed trees and a greater mean DBH than mature sites (Table 2.2). The same was true for old jack pine sites except that they had a lower density of jack pine trees than mature sites and the density of deciduous trees was not used to classify old and mature jack pine sites (Table 2.2). In total 2 mature white spruce and 2 mature jack pine sites had vegetation characteristics that resembled old growth sites more than mature sites, including the mature white spruce and jack pine site where I had detected Three-toed woodpeckers. The opposite was true for 3 old white spruce and 1 old jack pine site, although Three-toed woodpeckers were not detected at these sites.

Therefore, a reassessment of Three-toed woodpecker habitat occupancy based on the DFA revealed that again Three-toed woodpecker occupancy of old growth and recently burned coniferous forests was similar ($G=3.58$, $p = 0.635$). However, recently burned and old growth coniferous forests were occupied significantly more than mature coniferous forests ($G=24.63$, $p = 0.003$), since no Three-toed woodpeckers were detected at mature sites based on the new classifications (Figure 2.1).

Three-toed woodpecker presence in recently burned forests was negatively associated with the density of heavily burned and jack pine trees (Model $X^2 = 17.29$, $p < 0.001$, $R_N^2 = 0.37$). This model classified 46.2% of observed presences and 90.2% of absences correctly. At sites where Three-toed woodpeckers were detected, the mean

density of heavily burned and jack pine trees was (mean \pm SE) 5.4 ± 1.4 and $4.5 \pm 1.8 / 100 \text{ m}^2$ respectively (Appendix 2.1). Presence in old and mature coniferous forests was negatively associated with the density jack pine and standing trees and positively associated with the density of downed trees (Model $X^2 = 10.52$, $p = 0.02$, $R_N^2 = 0.18$). However, all three variables failed to correctly classify any of the observed Three-toed woodpeckers at a probability for entry into the model of both 0.10 and 0.15. A subsequent model including only old growth sites also failed to include any variables in the model.

2.3.1.2 Black-backed woodpeckers

Black-backed woodpeckers did not occupy any old growth or mature habitats within 50 km of the Mariana Lake post-fire forest (Figure 2.1). They were only detected in recently burned coniferous forests and their numbers did not differ between burned white spruce, black spruce and jack pine habitats ($G=0.711$, $p = 0.717$, Figure 2.1). However, Black-backed woodpecker presence or absence could not be predicted by any of the vegetation variables with a probability for entry into the model of 0.10 or 0.15.

2.3.2 Distance from recently burned forests

Vegetation characteristics of 75 km and 150 km old black spruce sites differed significantly as did 75 km and 150 km old white spruce sites (Wilk's Lambda = 0.68, $p = 0.02$ and Wilk's Lambda = 0.40, $p < 0.001$, Table 2.2). In both cases the density of standing and downed trees was greater at sites 75 km from recently burned forests than 150 km. The density of black spruce trees was higher at 75 km than 150 km black spruce sites and 150 km white spruce sites had a greater mean DBH than 75 km sites (Table 2.2). Therefore, using a randomized G-test to examine the effect of distance on woodpecker habitat occupancy would have been confounded by differences in vegetation between the two locations. Hence, I used a single logistic regression model to examine the effects of distance and vegetation on woodpecker occupancy of 75 km and 150 km black and white spruce sites respectively.

Three-toed woodpecker presence or absence at 75 km and 150 km black spruce sites (Figure 2.2) could not be predicted by either the distance variable or vegetation variables with a probability for entry into the model of 0.10 or 0.15. Presence at 75 km and 150 km white spruce sites (Figure 2.2) was positively associated with the density of

black spruce trees (Model $X^2 = 3.13$, $p = 0.08$, $R_N^2 = 0.107$), which correctly classified 18.2% of presences and 96.7% of absences, but the distance variable failed to predict occupancy.

Black-backed woodpecker presence at 75 km and 150 km black spruce sites (Figure 2.2) was positively associated with the distance variable representing 150 km sites, density of deciduous and standing trees and mean DBH (Model $X^2 = 27.19$, $p < 0.001$, $R_N^2 = 0.81$). These variables correctly predicted 85.7% of presences and 94.1% of absences. Old black spruce sites occupied by Black-backs had a mean density of deciduous and standing trees of (mean \pm SE) 3.0 ± 1.4 and $60.3 \pm 6.2 / 100 \text{ m}^2$ respectively and a mean DBH of 162.0 ± 19.3 (Appendix 2.1). Black-backed presence at white spruce sites 75 km and 150 km from recently burned forests (Figure 2.2) was negatively associated with the density of deciduous trees (Model $X^2 = 4.40$, $p = 0.04$, $R_N^2 = 0.50$). However, this variable failed to correctly predict any of the observed presences at a probability for entry into the model of 0.10 or 0.15.

2.3.3 Occupancy of different aged post-fire forests

2.3.3.1 Three-toed woodpeckers

Three-toed woodpeckers were present in the 3, 4 and one of the two 8 year post-fire forests and their occurrence decreased significantly between 3 and 8 years post-fire ($G=4.574$, $p = 0.052$, Figure 2.3). Presence in the 3, 4 and 8 year post-fire forests was negatively associated with the density of moderately burned and jack pine trees and positively associated with the density of lightly burned trees (Model $X^2 = 20.61$, $p < 0.001$, $R_N^2 = 0.40$). These variables classified 30% of Three-toed presences and 98.8 % of absences correctly. At sites where Three-toed woodpeckers were detected, the mean density of moderately burned, jack pine and lightly burned trees was (mean \pm SE) 21.8 ± 4.1 , 3.6 ± 1.3 and $21.5 \pm 10.7 / 100 \text{ m}^2$, respectively.

2.3.3.2 Black-backed woodpeckers

Black-backed woodpeckers were detected in the 3, 4 and both 8 year post-fire forests and their occurrence was not significantly different between these different aged burns ($G=3.34$, $p=0.359$, Figure 2.3). Black-backed woodpecker presence in 3, 4 and 8 year post-fire forests was best explained by the proportion of severely burned trees (Model $X^2 = 5.93$, $p = 0.02$, $R_N^2 = 0.08$). This variable correctly predicted 29 % of

Black-backed presences and 85.4% of absences. Black-backs occupied sites where the mean density of severely burned trees was (mean \pm SE) $9.6 \pm 1.7/100\text{ m}^2$.

2.3.3.3 Insect biomass

Wood-boring insect biomass and total insect biomass did not differ between the 3, 8 and 16 year post-fire forests sampled ($K-W$, $X^2 = 2.01$, $p = 0.366$, $X^2 = 3.15$, $p = 0.207$). Bark beetle biomass differed between post-fire forests ($K-W$, $X^2 = 6.07$, $p = 0.048$), but no differences were detected between post-fire forests based on subsequent multiple comparison tests (Tukey, $Q = 2.19$, $p > 0.10$, $Q_{0.10, \infty, 3}$, $Q = 0.132$, $p > 0.10$, $p < 0.10$, $Q_{0.10, \infty, 3}$, and $Q = 2.23$, $p > 0.10$, $p < 0.10$, $Q_{0.10, \infty, 3}$) (Table 2.4).

2.4 Discussion

2.4.1 Habitat association surveys

Three-toed woodpecker occupancy of burned and old growth coniferous forests was similar. This woodpecker species feeds primarily on bark beetle larvae (Scolytidae) directly beneath the bark layer of recently dead trees in both burned and unburned forests (Beal 1911, Goggans et al. 1989, Murphy and Lehnhausen 1998). However, recently dead trees are at a much higher density in recently burned forests than old growth conifer forests (Table 2.5). Density of Three-toed woodpeckers was higher in burned forests than the surrounding unburned forests in 3 other studies (see Caton 1996, Hoffman 1997, Murphy and Lehnhausen 1998). I did not look directly at density of birds, but the birds located within the burned area were in a much smaller area than those in the surrounding unburned forests. However, without any data on the reproductive success of birds in burned and unburned forests I do not have adequate information to comment on the quality of one habitat type over the other. Therefore, both recently burned and unburned coniferous forests are likely to be important to this species in boreal Alberta.

My initial hypothesis was that Three-toed woodpeckers would be found only in old and burned coniferous forests and not mature forests, due to a lack of sufficient foraging and nesting sites in mature forests (see Goggans et al. 1989, Steeger et al. 1993, Angelstam and Mikusinski 1994, Murphy and Lehnhausen 1998). Contrary to my hypothesis, Three-toed woodpeckers were detected in mature coniferous forests. However, both the mature white spruce and mature jack pine site (stand origin 1930 and 1900 respectively) where I detected Three-toed woodpeckers, had vegetation

characteristics that resembled more closely old growth than mature sites. Therefore, a reanalysis of occupancy data with these revised classifications revealed that Three-toed woodpeckers were only detected in recently burned and old growth forests, and not mature coniferous forests. I did not collect tree core data from these sites and thus, it is difficult to determine whether these sites were aged incorrectly from airphoto interpretation or whether they were a result of variability in site conditions. These forest inventory maps were generated initially as a forestry tool not a wildlife management tool, therefore if the intention of forest managers is for fine filter species specific management a more detailed tool may be needed.

Therefore, I do not recommend that Phase 3 Forest Inventory maps and associated stand ages be used to manage for Three-toed woodpeckers in unburned forests. Instead I believe that management should be based on structural characteristics not stand age. I have summarized the vegetation characteristics of unburned sites where Three-toed woodpeckers were detected in Appendix 2.2., which can be used at the stand level to predict suitable Three-toed woodpecker habitat. If in certain circumstances stand ages must be used for management purposes I recommend that unburned white spruce, black spruce and jack pine stands older than 110 years be managed for Three-toed woodpecker habitat.

In unburned mature and old coniferous forests I was unable to predict Three-toed presence with any certainty. Unfortunately, I did not accurately measure the number of wood-boring insects and bark beetles at each site, which is probably key to predicting presence or absence. Sites that were close to identical in structural and species composition were not occupied consistently, perhaps due to the patchy nature of insect infestations (Alberta Environmental Protection 1999). The second problem is that I did not measure any landscape variables such as patch size and adjacency that may have affected the occupancy of a site.

Three-toed woodpeckers have a circumboreal distribution overlapping the distribution range of spruce (Bock and Bock 1974). In recently burned forests they forage primarily on lightly burned trees (Murphy and Lehnhausen 1998) where bark beetles are most abundant, because the moisture content of the bark and phloem is too low in heavily burned trees (Werner and Post 1985). Therefore, it is not surprising that I

found that Three-toed woodpecker presence was negatively associated with the density of heavily burned trees and jack pine trees. While foraging Three-toed woodpeckers flake the bark off trees (see Murphy and Lehnhausen 1998) and due to their bill morphology they are not strong excavators (Spring 1965). Therefore, because jack pine trees have thicker bark than spruce trees (Farrar 1995), energetically they may represent a less suitable foraging substrate than spruce.

Black-backed woodpeckers were only detected in recently burned forests and they were equally numerous in white spruce, black spruce and jack pine forests. This is consistent with numerous studies that documented the association of this species with recently burned forests (Bourdo and Hesterberg 1951, Blackford 1955, Apfelbaum and Haney 1981, Harris 1982, Hutto 1995, Caton 1996, Villard and Schieck 1996, Hoffman 1997, Murphy and Lehnhausen 1998). However, I was unable to predict their presence or absence in recently burned forests with any vegetation variables. Perhaps a more detailed insect sampling protocol, that quantified insect availability at each site, may have increased my ability to predict Black-backed presence or absence.

2.4.2 Woodpecker occupancy of unburned old coniferous forests 75 km and 150 km from recently burned areas greater than 200 ha.

The Black-backed woodpecker has definitely been found far more often in recently burned forests than old unburned forests (Apfelbaum and Haney 1981, Caton 1996, Hoffman 1997, Murphy and Lehnhausen 1998), but they do inhabit and breed in non-burned forests (Goggans et al. 1989, Villard 1994, Weinhagen 1998). I hypothesised that the reason why I had detected no birds in the unburned forests within 50 km of the Mariana Lake fire was because they had recruited into the recent burn, to an area of higher food availability and nesting sites (see Blackford 1955, Villard and Schieck 1996, Murphy and Lehnhausen 1998). To quantify this hypothesis, I sampled old growth white and black spruce dominated sites 75 km and 150 km from recently burned forests greater than 200 ha for the presence of both species. The distance variable did not predict Three-toed woodpecker occupancy of 75 km or 150 km old growth white spruce or black spruce sites nor did it predict Black-backed woodpecker occupancy of 75 km and 150 km white spruce sites. However, Black-backed woodpecker presence in old growth black spruce sites was positively associated with the categorical variable representing the 150 km sites.

In addition, Black-backed woodpecker presence in old black spruce sites was positively associated with the density of deciduous and standing trees and mean DBH. Black-backed woodpeckers are conifer specialists (Boch and Boch 1974, Villard 1994) and are not known to use deciduous trees as a foraging substrate (Villard and Beninger 1993, Villard 1994). However, the sites where Black-backed woodpecker presence was correctly predicted by the density of deciduous trees, were black spruce dominated stands with less than 25% aspen. Therefore, the presence of this variable in the model indicates that black spruce dominated stands with an aspen component are suitable habitat for Black-backed woodpeckers. Previous studies have shown that Black-backed woodpeckers nest in areas of dense large diameter trees (see Caton 1996, Saab and Dudley 1998), possibly explaining why I found that presence in old black spruce forests was positively associated with the density of standing trees and mean DBH.

Based on the DFA, 75 km black spruce sites had a higher density of standing, downed and black spruce trees than 150 km sites. Therefore, because the variables that predicted Black-backed woodpecker presence were not the same as those that discriminated between 75 km and 150 km sites, there is an effect of distance from recently burned forests on the occupancy of old growth black spruce forests. However, there may have been larger landscape level effects of adjacency and patch size confounding the question of distance from recently burned forests and Black-backed woodpecker occurrence. Therefore, to accurately comment on the relationship between habitat occupancy and distance from recently burned forests landscape level effects of adjacency and patch size need to be examined as well as a larger number of locations at a greater number of distances from recently burned areas. Furthermore, future research could be designed to examine the relationship between habitat occupancy and distance from recently burned areas of varying sizes.

2.4.3 Black-backed and Three-toed woodpecker occupancy of different aged post-fire forests

Three-toed woodpecker numbers decreased between 3 and 8 years post-fire and their presence in 3, 4 and 8 year post-fire forests was best explained by a negative association with the density of moderately burned trees and jack pine trees and a positive association with the density of lightly burned trees. Lightly burned trees have the highest

abundance of bark beetles, the primary food source of Three-toed woodpeckers (Murphy and Lehnhausen 1998). The density of jack pine was also a negative predictor of Three-toed presence in recently burned forests. Again, I believe that because jack pine trees have a thicker bark than spruce (Farrar 1995) and Three-toed woodpeckers forage primarily by scaling the bark from trees, energetically jack pine may represent a less suitable foraging substrate than spruce.

Black-backed woodpeckers occupied post-fire forests longer than was initially hypothesised (see Hutto 1995, Murphy and Lehnhausen 1998). They were equally numerous between 3 and 8 years post-fire, but numbers decreased significantly between 8 and 16 years post-fire. The proportion of severely burned trees (100% burn 0-50% bark intact) best explained their presence within 3, 4 and 8 year post-fire forests. However this model only accounted for 29% of the presences, and explained only 8% of the variation in woodpecker presence or absence. The sites that were correctly predicted were primarily from the 8 year post-fire forests. Black-backed woodpeckers feed primarily on wood-boring insect larvae (Cerambycidae and Buprestidae) which are found in the sapwood of the tree (Richmond and Lejeune 1945, Murphy and Lehnhausen 1998). As the bark begins to peel and the tree begins to dry out, the suitability to wood-boring insects post-fire decreases (Werner and Post 1985). If the bark remained on the base of the tree, where it is thickest (J. Hoyt personal observation), the moisture content in this region of the tree may have remained high enough for severely burned trees to sustain populations of wood-boring insects for 8 years (see chapter 3).

I found no differences in bark beetle, wood-boring and total insect biomass between different aged burns, which was not consistent with the patterns of woodpecker occupancy of different aged post-fire forests. However, I do not feel that with the insect data collected I had the ability to adequately test my hypothesis that food availability would be limiting the persistence of woodpeckers in post-fire forests. In the 3 and 8 year post-fire forests the number of wood-boring insect larvae were probably underestimated because the larvae were concentrated in the lower 10 cm of the tree and sampling took place above this level (see chapter 3). Furthermore only 32 trees were sampled from a single location within each burn and insect infestations in large fires can be very patchy,

increasing the chances that the area sampled may not have been representative of the entire burned area (Alberta Environmental Protection 1999).

Recent studies from the northwestern United States reported that Black-backed woodpeckers nested at sites where snag density post-fire was the highest (155.0 ± 47.5 trees $> 23\text{cm}$ per ha) (see Saab and Dudley 1998). In my study there was no clear trend of decreasing density of standing dead trees with increasing age post-fire (Table 2.5). However, I did find that the proportion of standing dead trees in both the 16 and 17 year post-fire forests were significantly less than both 8 year post-fire forests and the 3 and 4 year post-fire forests (J. Hoyt unpublished data). Therefore, it is not clear if snag density is controlling post-fire occupancy. However, I do not wish to dismiss the hypothesis that food availability post-fire is limiting post-fire occupancy by Black-backed woodpeckers. Between 8 and 16 years post-fire there is likely a point at which it is no longer profitable to occupy post-fire forests due to increased predation risk in the more open forest and decreased food availability. However to adequately comment on this idea further research is needed.

The question still remains as to why I found that Black-backed woodpeckers occupied post-fire forests longer than previously reported (see Blackford 1955, Villard and Beninger 1993, Hutto 1995, Murphy and Lehnhausen 1998). In chapter 3, I reported that Black-backed woodpeckers selected jack pine for foraging more than would have been expected by random in the 3 year post-fire forest. I attributed this to the fact that jack pine has a thicker bark than spruce (Farrar 1995) and therefore retains more moisture and remains more suitable to wood-boring insects for a longer period post-fire than spruce. Murphy and Lehnhausen (1998) found no Black-backed woodpeckers after 4 years-post fire in a burn that was composed of over 90% spruce and no jack pine. Therefore, I feel that the presence of jack pine in the post-fire forests that I studied contributed to the prolonged occupancy of these forests by Black-backed woodpeckers.

However, density or numbers of individuals may not be an appropriate measure of habitat quality (Van Horne 1983). Simply because I observed equal occurrence of Black-backed woodpeckers in 3 and 8 year post-fire forests does not necessarily mean that these two habitats are equally suitable. It could be that 8 year post-fire forests represent a sink habitat, where mortality is higher than natality (Pulliam and Danielson 1991) and the

birds that occupy these habitats are either juveniles or floaters. However, it is unlikely that if the 8 year post-fire forests were a sink habitat I would have found densities higher than would normally be found in unburned coniferous forests. It is more likely that, although the numbers were similar between the 3 and 8 year post-fire forests, the 8 year post fire forest may be less productive than the 3 year post-fire forest or a 1 or 2 year post-fire forests, due to changes in food availability. However, further research is needed both in the area of productivity and food availability differences between different aged post-fire forests.

2.4.4 Evaluation of logistic regression models used to predict Three-toed and Black-backed woodpecker presence or absence

Due to the nature of my sampling design my ability to predict woodpecker presences was limited. Since I visited each site only once it is possible that a site represented suitable woodpecker habitat and was occupied by a woodpecker, but I did not detect it because it was outside the broadcast radius. Had sites been resampled my ability to detect woodpeckers would have been enhanced. Therefore, it is not surprising that with the exception of one model, logistic regression models used to predict Three-toed and Black-backed woodpecker presence or absence, failed to predict more than 50% of observed presences correctly. Furthermore, variables that entered the model explained less than 40%, to a minimum of 7%, of the variation in woodpecker presence or absence. Although it would appear that I have accounted for only a small proportion of the variation in presence or absence using these models, the actual predictive ability of the models may be much higher simply because my overall ability to detect a presence was low. However, I do believe that obtaining an index of insect availability at each site would have increased the predictive ability of my models. I had hoped that vegetation measurements would be indirect measures of insect availability, but in the future actual measures of insect abundance would be best. Furthermore future studies should be designed to incorporate landscape level factors such as patch size and adjacency which may be influencing insect abundance and hence woodpecker presence or absence.

2.4.5 Burn dependency of Black-backed woodpeckers

In recent years numerous studies have suggested that Black-backed woodpeckers are burn dependent (Hutto 1995, Caton 1996, Murphy and Lehnhausen 1998, Saab and

Dudley 1998). Murphy and Lehnhausen (1998) conclude that Black-backed woodpecker numbers increase when recently burned forests are occupied because they recruit into these habitats and reproduce well there, and numbers decrease when occupying unburned forests because they are seemingly rare in old or mature unburned forests. However in my study, Black-backed woodpeckers were detected at 6 of 22 old black spruce sites surveyed (27.3% occupancy) in the Calling Lake region, which is similar to the % occupancy observed in the Mariana Lake fire for white spruce, black spruce and jack pine habitats (40.9, 30 and 40.9 % respectively). There has been very little work done previously in black spruce, therefore I have to question whether the principle of Murphy and Lehnhausen (1998) can be applied equally to all unburned habitats, particularly old black spruce.

However, to asses the source-sink dynamics of recently burned and old growth black spruce habitats estimates of fecundity and survival would be required (Pulliam and Danielson 1991). Survival estimates would be the most difficult to obtain, but recently fibre optics cameras have made it much easier to examine the contents of nest cavities and thus determine fecundity. In the two years of my study a total of 22 Black-backed woodpecker nests were located in the recently burned forests. Although I did not locate any nests in unburned forests, I believe that with an intensified search effort it would be possible to find nests in unburned forests (see Weinhagen 1998). Therefore, I believe that old growth black spruce sites embedded in a matrix of old forests need to be examined more closely before they can be classified as sink habitat.

2.4.6 Future research questions

Even if old growth black spruce habitats are not sink habitats, it is quite likely that population persistence of Black-backed woodpeckers will depend on the frequency of recently burned forests within their dispersal range (see Thomas 1994, Hutto 1995, Murphy and Lehnhausen). However, without knowing whether old black spruce sites are source or sink habitats it is difficult to comment on how these habitats will affect population persistence. In addition, for future modeling exercises it would also be useful to determine at any one point in time what proportion of the landscape was old growth black spruce versus recently burned forests (0-8 years). These data would provide an indication as to which type of habitat contains the most Black-backed woodpeckers at

any one time and also whether there are prolonged periods where recently burned forests are absent from the landscape. Furthermore, there are still numerous questions that need to be examined with respect to recently burned forests. For example: What is the relationship between fire size and population density? Murphy and Lehnhausen (1998) stated that large fires could be detrimental to Black-backed woodpeckers since these fires destroy secondary habitat (unburned forests) and only the perimeter of these fires are occupied by Black-backed woodpeckers. However, I found Black-backed woodpeckers throughout the entire burned area up to 8 years post-fire, ranging from 1 km to greater than 20 km from the edge of the fire. Another important question is how far will individuals of this species disperse into recently burned habitat. Recent advancements in the use of stable carbon isotopes to link winter and summer events in a migrating bird could possibly be used to track populations of Black-backed woodpeckers between recently burned forests (Marra et al. 1998).

2.4.7 Conclusions

Three-toed woodpeckers were detected in old growth, mature and recently burned coniferous forests and their occupancy of recently burned forests decreased significantly between 3 and 8 years post-fire. However, mature forest sites where birds were detected resembled more closely the vegetation characteristics of old sites than mature sites. Therefore, I do not recommend that Phase 3 Forest Inventory maps and associated stand ages be used to manage for Three-toed woodpeckers in unburned forests. Instead I believe that management should be based on structural characteristics not stand age. Black-backed woodpeckers were only detected in recently burned areas within a 50 km of the Mariana Lake fire. Although, they were detected in old growth black spruce forests at a distance of 150 km form recently burned forests and their occupancy of these sites appears to be related to the effect of distance from recently burned forests. However, further research is needed to clarify this finding. Furthermore, without research designed to examine the productivity of Black-backed woodpeckers in recently burned forests and old growth black spruce forests it is difficult to comment on the possible source sink dynamics of these two habitats. Black-backed woodpeckers were detected in 3, 4 and 8 year post-fire forests, but not 16 or 17 year post-fire forests. However, it was not clear if their occupancy of these forests was limited by food availability and a more detailed

insect sampling protocol is needed to address this question. Furthermore, in all habitat types vegetation data only explained a small proportion of the variation in woodpecker presence or absence, possibly due to the inability to accurately predict insect abundance at a site. Therefore, a more detailed insect sampling protocol in recently burned and unburned forests would likely improve one's ability to predict woodpecker occupancy of burned and unburned habitats.

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Table 2.1 Characteristics of post-fire forests sampled in 1998 for Black-backed and Three-toed woodpecker presence or absence.

Year of Burn	Years Post-fire	Fire Number	Fire Size	# Sites	Sampling Dates (1998)
1995	3	DL1-009-95	135072.05 ha	24	April 3 – 23
1994	4	DA1-5-94	2160 ha	22	April 4 – 23
1990a	8	DL2-066-90	10832 ha	23	April 5 – 24
1990b	8	DL4-040-90	9438 ha	24	April 4 – 22
1982	16	DL4-17-82	28245.04 ha	21	April 4 – 22
1981	17	DL4-16-81	8354 ha	24	April 5 – 23

Table 2.2. Results of discriminant function analysis tests of equality of group means for comparisons of mature and old white spruce and jack pine sites and old black spruce and white spruce sites 75 km and 150 km from recently burned areas > 200 ha. All predictor variables except mean DBH (MDBH) represent density (# of trees / 100 m² of transects) at each site, and all variables were calculated using only those trees > 55 mm DBH. Variables for the analysis of 75 km and 150 km white spruce sites were log transformed to meet the assumptions of normality. Variables are as follows: SW = white spruce, PJ = jack pine, and SB = black spruce, DECID = deciduous, SPR = spruce (white and black spruce), RDT = recently dead trees, MDBH = mean DBH, STAND = density of standing trees and DOWN = density of downed trees. Significant differences ($p < 0.10$) are presented in bold.

Analysis	Variables	Mean (STD)	Wilk's Lambda	F Value	DF (1,2)	Significance
Mature vs. Old	SW	25.4 (11.7) vs. 22.6 (6.4)	0.98	0.84	1,40	0.36
White Spruce	DECID	10.3 (6.1) vs. 7.1 (4.0)	0.91	3.88	1,40	0.06
	RDT	5.4 (5.0) vs. 4.0 (2.6)	0.97	1.36	1,40	0.25
	MDBH	185.6 (40.8) vs. 261.4 (56.7)	0.62	25.05	1,40	> 0.01
	STAND	41.8 (12.2) vs. 33.4 (6.7)	0.84	7.54	1,40	0.01
	DOWN	0.4 (1.2) vs. 1.8 (2.2)	0.87	5.93	1,40	0.02
Mature vs. Old	PJ	38.0 (22.2) vs. 21.6 (8.2)	0.81	10.62	1,44	< 0.01
Jack Pine	SPR	20.9 (12.5) vs. 20.1 (16.6)	0.10	0.03	1,44	0.87
	RDT	5.2 (5.0) vs. 4.3 (2.9)	0.99	0.58	1,44	0.45
	MDBH	125.1 (31.0) vs. 214.8 (49.1)	0.44	55.81	1,44	< 0.01
	STAND	56.1 (18.7) vs. 34.4 (11.8)	0.67	21.56	1,44	< 0.01
	DOWN	8.3 (9.8) vs. 14.0 (12.4)	0.94	2.99	1,44	0.09
75 km vs. 150 km	SB	65.4 (21.7) vs. 52.6 (19.0)	0.91	4.08	1,39	0.05
Black Spruce	RDT	9.5 (7.6) vs. 9.7 (8.1)	1.00	0.01	1,39	0.95
	MDBH	146.4 (28.2) vs. 137.6 (33.0)	0.98	0.84	1,39	0.37
	STAND	65.6 (17.9) vs. 52.3 (13.7)	0.84	7.14	1,39	0.01
	DOWN	11.4 (10.8) vs. 5.9 (8.0)	0.92	3.47	1,39	0.07

75 km vs. 150 km	LOG_SW	1.30 (0.46) vs. 1.24 (0.29)	0.99	0.25	1.39	0.62
White Spruce	LOG_DECID	0.70 (0.42) vs. 0.89 (0.32)	0.93	2.88	1,39	0.01
	LOG_RDT	0.60 (0.38) vs. 0.62 (0.28)	1.00	0.01	1,39	0.92
	LOG MDBH	231.4 (51.9) vs. 270.8 (45.6)	0.85	6.70	1,39	0.01
	LOG_STAND	1.61 (0.14) vs. 1.49 (0.03)	0.76	12.56	1,39	> 0.01
	LOG_DOWN	0.86 (0.34) vs. 0.36 (0.30)	0.62	24.29	1,39	> 0.01

Table 2.3 List of independent variables used in logistic regression analyses to predict Black-backed and Three-toed woodpecker presence or absence. All predictor variables except mean DBH (MDBH) represent density (# of trees / 100m² of transects) at each site, and all variables were calculated using only those trees > 55 mm DBH. The species column indicates whether the variables were used in analyses for Black-backed (BBWO) or Three-toed woodpeckers (TTWO) or both species. When variables were highly correlated ($r > 0.70$) I ran simultaneous models with correlated variables in different models.

Analysis	Sites Used in the Analysis	Species	Variables	Description of Variables
Recently Burned Forests	White spruce, black Spruce and jack pine	BBWO / TTWO	SPR SB SW PJ DECID LBURN MBURN	Spruce (white spruce and black spruce) Black spruce White spruce Jack pine Deciduous, aspen balsam poplar and birch Light burn (1-80% burn, 100% bark intact) Moderate burn (100% burn, 80-100% bark intact)
Different Aged Post-Fire Forests	3, 4, and both 8 year post-fire forests	BBWO / TTWO BBWO / TTWO BBWO / TTWO BBWO / TTWO	HBURN DBH147 MDBH DOWN STAND	Heavy burn (100% burn, 0-80% bark intact) DBH > 147 mm Mean DBH Downed trees Standing trees
		BBWO / TTWO BBWO / TTWO BBWO / TTWO	SPR SB SW PJ	Spruce (white spruce and black spruce) Black spruce White spruce Jack pine
		BBWO / TTWO BBWO / TTWO	DECID	Deciduous, aspen balsam poplar and white birch
		LBURN MBURN		Light burn (1-80% burn, 100% bark intact) Moderate burn (100% burn, 80-100% bark intact)

		BBWO / TTWO	H BURN	Heavy burn
		BBWO / TTWO	S BURN	100% burn, 50-80% bark intact
		BBWO	DBH147	Severe burn (100% burn, 0-50% bark intact)
		BBWO / TTWO	MDBH	DBH > 147 mm
		BBWO / TTWO	DOWN	Mean DBH
		BBWO / TTWO	STAND	Downed trees
				Standing trees
Old and Mature	Old and mature,	TTWO	SPR	Spruce (white spruce and black spruce)
Coniferous	white spruce, black	TTWO	SB	Black spruce
Forests	Spruce and jack pine	TTWO	SW	White spruce
		TTWO	PJ	Jack pine
		TTWO	DECID	Deciduous, aspen balsam poplar and birch
		TTWO	RDT	Recently dead trees (Class 11 and 12)
		TTWO	MDBH	Mean DBH
		TTWO	DOWN	Downed trees
		TTWO	STAND	Standing trees
Sites 75 km and	Old white and black	BBWO / TTWO	SPR	Spruce (white spruce and black spruce)
150 km From	Spruce sites	BBWO / TTWO	SB	Black spruce
Recently Burned		BBWO / TTWO	SW	White spruce
Forests > 200 ha		BBWO / TTWO	PJ	Jack pine
		BBWO / TTWO	DECID	Deciduous, aspen balsam poplar and birch
		BBWO / TTWO	RDT	Recently dead trees (Class 11 and 12)
		BBWO	DBH147	Trees > 147 mm DBH
		BBWO / TTWO	MDBH	Mean DBH
		BBWO / TTWO	DOWN	Downed trees
		BBWO / TTWO	STAND	Standing trees
	Dummy			A categorical variable used to code 75 km (0) and 150 km (1)

Table 2.4 Mean insect biomass data for 3, 8b and 16 year post-fire forests. Mean biomass was generated from totals of basal, middle and top sections of 16 black spruce and 16 jack pine trees in each post-fire forest. Mean biomass (mg \pm SE) is presented for bark beetle, woodborer, and total biomass (bark beetle + woodborer) in each post-fire forest.

Years Post-Fire	Type of Biomass	Biomass Mean (mg) \pm SE
3	Bark beetle biomass	0.87 (0.30)
	Wood-borer biomass	15.37 (5.70)
	Total biomass	16.24 (5.76)
8	Bark beetle biomass	0.20 (0.18)
	Wood-borer biomass	3.84 (1.72)
	Total biomass	4.04 (1.73)
16	Bark beetle biomass	1.26 (0.59)
	Wood-borer biomass	7.97 (6.49)
	Total biomass	9.22 (6.46)

Table 2.5 Mean density of recently dead trees in recently burned forests and old growth coniferous forests. Mean density (# trees / 100 m² of transects) of recently dead trees was calculated based on totals from each site in each habitat type and is based on only those trees > 55 mm DBH.

Forest Type	Habitat Type	# of Sites	Mean Density of Recently Dead Trees
Recently burned	White spruce	22	32.9
	Black spruce	20	47.3
	Jack pine	22	41.9
Old growth coniferous	White spruce	61	4.1
	Black spruce	64	11.1
	Jack pine	23	4.3
Post-fire forests	3-years post-fire	24	57.3
	4-years post-fire	22	40.5
	8-years post-fire	23	37.2
	8-years post-fire	24	59.9
	16-years post-fire	22	34.3
	17-years post-fire	24	31.0

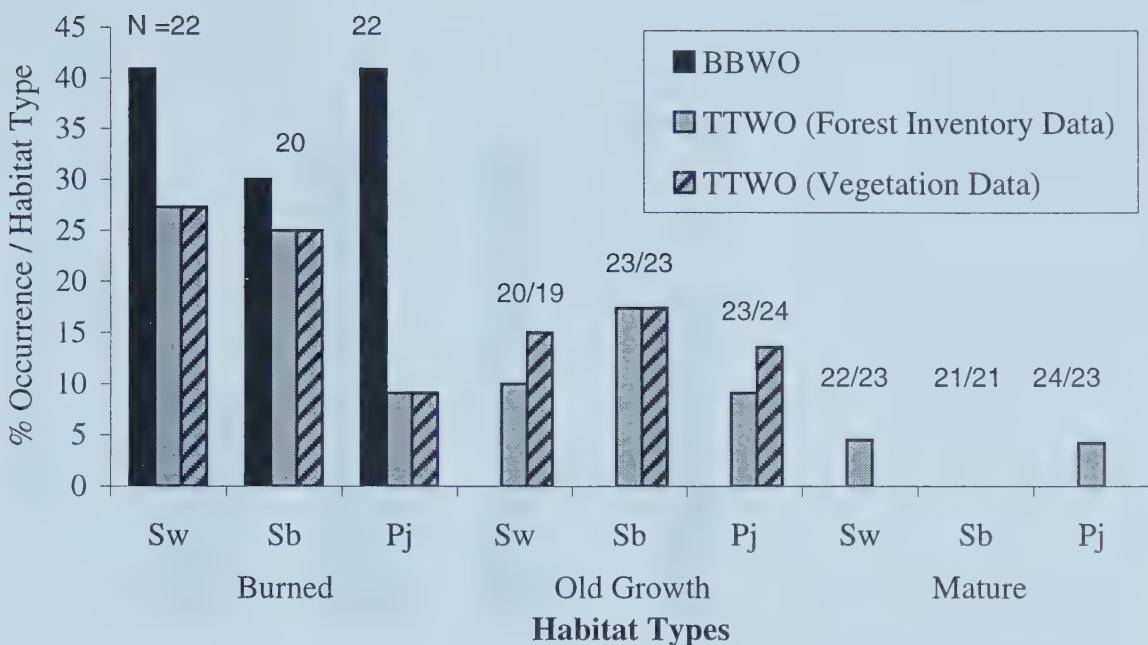


Figure 2.1. % Occurrence of Black-backed (BBWO) and Three-toed woodpeckers (TTWO) in recently burned, old growth and mature coniferous forests in 1997 and 1998. Data are presented for TTWO occupancy of sites based on stand ages obtained from Phase 3 Forest Inventory data and reclassified sites based on the discriminant function analysis of vegetation data. N represents the number of sites surveyed in each habitat. When two numbers are present the first represents the N for Forest Inventory Data and the second for reclassified sites based on Vegetation Data. Sw = white spruce, Sb = black spruce, Pj = jack pine.

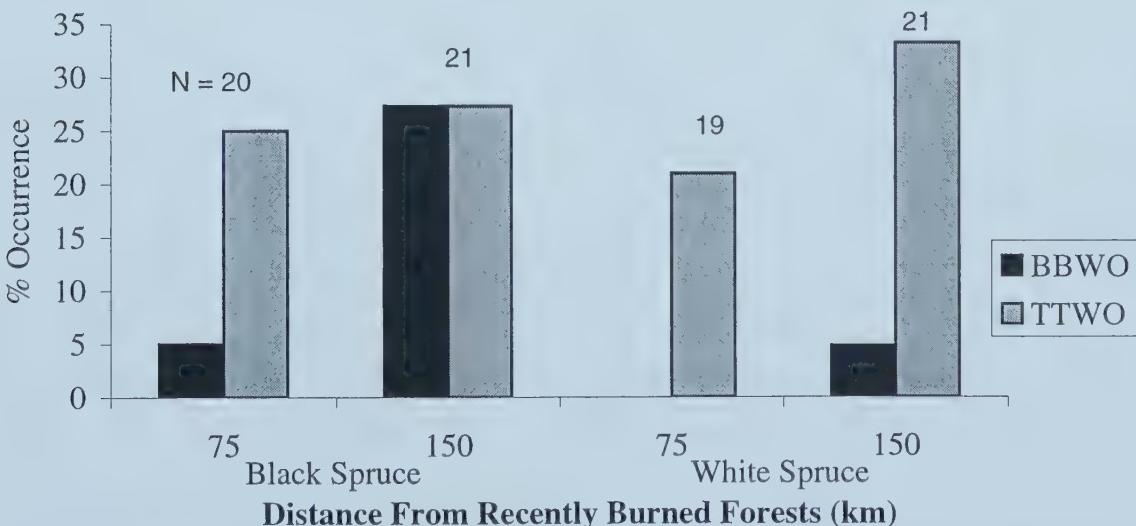


Figure 2.2 % Occurrence of Black-backed (BBWO) and Three-toed woodpeckers (TTWO) in old growth white and black spruce sites 75 km and 150 km from recently burned forests greater than 200 ha in 1998. N represents the number of sites surveyed in each habitat.

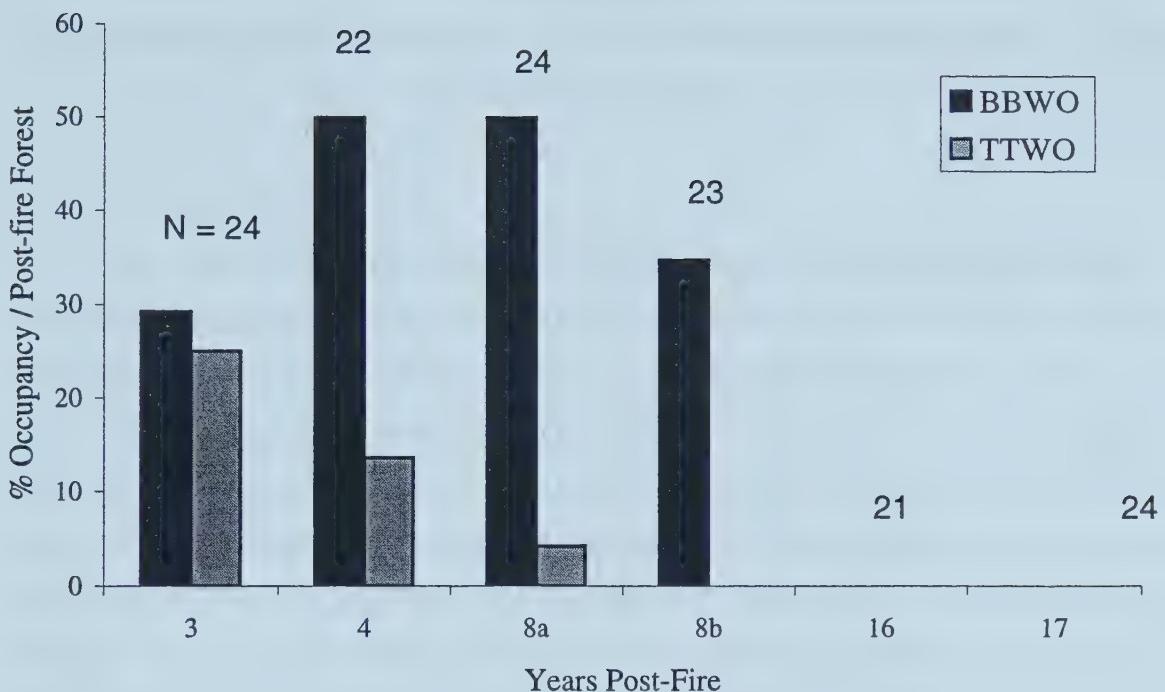


Figure 2.3 % Occupancy of Black-backed (BBWO) and Three-toed woodpeckers (TTWO) in post-fire forests aged 3, 4, 8, 8, 16 and 17, years post-fire in 1998. N represents the number of sites surveyed in each post-fire forest.

CHAPTER 3

FORAGING ECOLOGY OF BLACK-BACKED WOODPECKERS IN A 3-YEAR POST-FIRE FOREST.

3.1 Introduction

Black-backed woodpeckers (*Picoides arcticus*) occupy recently burned conifer forests, exploiting outbreaks of wood-boring insects (Cerambycidae and Buprestidae) and bark beetles (Scolytidae) that invade following fire (Bourdo and Hesterberg 1951, Blackford 1955, Apfelbaum and Haney 1981, Villard and Beninger 1993, Hutto 1995, Hoffman 1997, Murphy and Lehnhausen 1998, Saab and Dudley 1998). Several studies have examined foraging tree use and foraging behavior of Black-backed woodpeckers in recently burned forests (see Villard and Beninger 1993, Murphy and Lehnhausen 1998). Foraging habitat appears to be selected at two scales, consistent with third and fourth-order habitat selection outlined by Johnson (1980). First, at the level of the foraging territory, trees used for foraging are selected from available trees within the surrounding area. Second, the height at which to forage on the tree is selected. Previous studies have examined the characteristics of trees used for foraging by woodpeckers (see Villard and Beninger 1993, Villard 1994, Murphy and Lehnhausen 1998), but did not compare selected trees to those available on the territory.

Sexual differentiation in foraging niches of birds has been well documented, especially for woodpecker species (Selander 1966, Kilham 1970, Hogstad 1978, Peters and Grubb 1983). Niche differentiation and differences in foraging ecology have been attributed to male dominance and sexual dimorphism in bill length (see Kilham 1965, Selander 1965, Peters and Grubb 1983, Morrison and With 1987, Matthysen et al. 1991). When food is limiting, co-existence of the sexes is only possible if morphological dimorphisms exist and or sexes exhibit behavioral differences that result in resource partitioning (see Wallace 1974, Hogstad 1976). However, when food is superabundant, such as during an insect outbreak, resource partitioning may not be as pronounced. Murphy and Lehnhausen (1998) found that, in a recently burned forest, Black-backed woodpecker sexes differed in foraging height and the degree of burn of the trees used for

foraging, but no differences were found with respect to foraging techniques, tree species or circumference of trees used for foraging.

Recently burned forests represent suitable habitat for wood-boring insects and bark beetles due to the increased density of recently killed and dying timber upon which to feed (Parmalee 1941, Richmond and Lejeune 1945, Alberta Environmental Protection 1999). Murphy and Lehnhausen (1998) analyzed the stomach contents of several Black-backed woodpeckers occupying recently burned forests to determine that they were foraging primarily on wood-boring beetle larvae (*Monochamus sp.*) (see also Beal 1911, Villard and Beninger 1993). The authors also conducted coarse-scale insect sampling and found that wood-boring beetle larvae were most abundant in fire-killed spruce trees, where the majority of foraging observations occurred.

I examined Black-backed woodpecker foraging tree selection and foraging behavior in a 3-year old burn in the boreal forest of Alberta. My first objective was to determine Black-backed woodpecker foraging habitat selection. I did this by measuring the tree species, burn classes, DBH classes, standing versus downed trees used for foraging by male and female Black-backed woodpeckers versus what would have been expected if they had foraged at random and by measuring the heights where birds foraged. The second objective was to examine differences in foraging tree selection and foraging behavior between male and female Black-backed woodpeckers. The final objective of the study was to conduct coarse-scale insect sampling in spruce and jack pine trees in an attempt to correlate insect infestation levels with woodpecker foraging habitat selection.

Based on previous studies, I predicted that Black-backed woodpeckers would forage primarily on burned conifer tree (*Picea* spp. and *Pinus* spp.); on moderately burned substrates, medium to large diameter trees and standing trees as opposed to downed trees (see Harris 1982, Villard and Beninger 1993, Villard 1994, Murphy and Lehnhausen 1998). My null hypothesis was that there would be no differences in use of trees versus their availability on the foraging territory. I expected differences between sexes with respect to foraging height and the burn classes of trees used for foraging (see Murphy and Lehnhausen 1998). Finally, I expected insect infestation to be highest in those species and foraging zones where the majority of foraging observations occurred.

3.2 Methods

3.2.1 Study area

This study was conducted in an area approximately 30 by 40 km in the Mariana Lake region of the northeastern boreal forest of Alberta ($55^{\circ} 5' N$, $111^{\circ} 55' W$) (Appendix I). The study area burned in April of 1995 in a 135,000 ha stand-replacing fire. Prior to burning this area was dominated by black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) with smaller patches of mixed-wood forest dominated by white spruce (*Picea glauca*) and aspen (*Populus tremuloides*) (Alberta Forestry, Lands and Wildlife 1985). Field work for this study was conducted during the spring and summer of 1998, 3-years post-fire. At this time the majority of the burned trees remained standing and there was very little tree regeneration greater than 1 m (J. Hoyt unpublished data).

3.2.2 Black-backed woodpecker foraging observations

Foraging observations of male and female Black-backed woodpeckers were conducted between 7 May and 7 June 1998; the nesting period for Black-backed woodpeckers in my study area. Between 7 and 21 May, most birds were incubating whereas most pairs were feeding young during the last two weeks of the observation period (see Appendix 3.1). Foraging observations were conducted on 17 different Black-backed woodpecker territories on which both the male and female were present. To ensure that all individuals were foraging within the burned area boundary, all territories were located at least 300 meters from the fire edge.

I located Black-backed woodpeckers by returning to sites where they had been detected during habitat association surveys earlier that spring (see Chapter 2) and by listening for foraging and call notes, which can be heard up to 75 m (personal observation). For 15 of the 17 territories nesting trees were located, making it possible to locate the birds by waiting at the nest for them to return. If birds could not be located by either of these methods, then a recording of a Black-backed woodpecker call-drumming was played for 1 to 2 minutes. After the playback I waited approximately 5 to 10 minutes before commencing foraging observations. Foraging observations were conducted by a total of four field assistants working in pairs and pairing was switched on a daily basis to minimise observer bias.

Foraging observations were recorded on a handheld tape recorder every 30 sec. At each territory females and males were observed until they had used between 20 and 25 trees for foraging. If the bird was temporarily lost for any one or several of the 30-second observations, it was recorded as out of sight and the observations began when it was relocated. If the bird was performing a behavior other than foraging (e.g. drumming, preening, calling and territorial defence) this behaviour was recorded. Whenever possible we tried to obtain the 20-25 trees used for foraging by males and females in a single observational period. However, on several occasions we had to return on a subsequent day to finish observations. When a bird was observed foraging, the sex of the bird, foraging zone on the tree and foraging technique were recorded (Villard and Beninger 1993, Villard 1994). Each tree that was used for foraging was marked with flagging tape for subsequent relocation to collect vegetation data.

Four foraging zones were defined: Zone 1 (deadwood on the ground), Zone 2 (lower one-third of the tree), Zone 3 (middle one-third of the tree) and Zone 4 (upper one-third of the tree). As well, three foraging techniques were defined: pecking (striking the bark with the bill and removing small pieces of bark), scaling (flaking the bark off the tree), and excavating (digging large or small holes in the wood).

3.2.3 Vegetation sampling

For each of the trees that were foraged on by male and female Black-backed woodpeckers, two random trees were chosen to examine differences between trees used for foraging and what would have been expected if foraging was random. These trees were located by using a list of random directions and distances, to pace a direction and distance (range: 1 to 100 meters) from the tree used for foraging.

The following vegetation variables were collected for each of the trees used for foraging by both sexes and for random trees: tree species; class (representing burn and decay classes); diameter at breast height (DBH) (in mm); and condition (indicating whether the tree was standing or had fallen down). Ten species were defined: white spruce, black spruce, aspen, jack pine, balsam poplar (*P. balsamifera*), white birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), alder (*Alnus sp*), tamarack (*Larix laricina*), and unknown species. Fifteen classifications were defined based on the degree of burn, state of decay and whether the tree was alive or dead, as follows: **1:** lightly

burned trees (1-80% burn, 100% bark intact); **2:** moderately burned trees (100% burn, 80-100% bark intact); **3:** heavily burned trees (100% burn, 50-80% bark intact); **4:** severely burned trees (100% burn, 0-50% bark intact); **5:** charred snag (0% bark and wood severely burned); **6:** burned stump < 50 cm; **7:** burn salvage logged stump; **8:** unburned, recently killed and twigs and leaves intact; **9:** unburned, recently killed, twigs and leaves lost and wood intact; **10:** unburned, dead, small branches lost and bark beginning to peel; **11:** unburned, dead and only major branches remain, < 20% bark peeling; **12:** unburned, dead, canopy broken and bark condition variable; **13:** unburned, dead decomposing stump < 4m and > 20% bark peeling; **14:** unburned, live and < 5% dead twigs and branches; **15:** unburned, live and 5-80% dead twigs and branches.

Diameter at breast height measurements taken in the field were later assigned to five different DBH classifications: DBH1 (≤ 35 mm), DBH2 (36-75 mm), DBH3 (76-150 mm), DBH4 (151-250 mm) and DBH5 (> 250 mm) (Villard and Beninger 1993, Villard 1994).

3.2.4 Insect sampling

Insect sampling was conducted between 15 and 25 July 1998 in the same 3 year old burn where foraging observations were conducted. A total of 32 trees was sampled: 16 black spruce and 16 jack pine. Trees selected were between 110 mm and 200 mm DBH, roughly coinciding with the 95% confidence intervals for the DBH of trees used for foraging. The 16 trees of each species were obtained equally from lightly, moderately and heavily burned trees since these burn classes represented the majority of available trees. Cutting, storage and preparation of tree sections and calculation of bark beetle and wood-boring insect biomass measures followed the same methodologies as outlined in Chapter 2 (see section 2.2.6). However, I also examined wood-boring insect galleries in each section. The total number of galleries of wood-boring insects in the sapwood was tabulated for each of the 10 slices and then totaled for the entire section. This method provided a coarse index of wood-boring insect activity in each of the three locations for each tree species.

3.2.5 Analyses

3.2.5.1 Tree characteristic and foraging observation data

Variables within each of the species, class, DBH class, foraging zone and foraging technique classifications that represented less than 4 % of the total number of trees observed and random trees, were not retained for future analyses. This was because they would not be normally distributed and their small percentages would provide very little predictive power in determining differences in tree characteristics or foraging observations between sexes or versus random trees. I combined white and black spruce into a single category, designated spruce, because wood-boring insects and bark beetles infesting white and black spruce are similar (Ives and Wong 1988). Therefore the following is a list of variables that were retained for future analyses: spruce; jack pine; burn class 1, 2, 3 and 4 (lightly, moderately, heavily and severely burned); DBH class 2, 3, 4 and 5; standing trees; all three foraging techniques; and all four foraging zones.

When calculating proportions for each of these variables, restrictions were used that trees had to be either spruce or jack pine; and class 1, 2, 3 or 4; and DBH class 2, 3, 4, or 5. For example the proportion of spruce trees used by the female at territory one was based on the number of spruce trees used that were class 1, 2, 3 or 4 and DBH class 2, 3, 4 or 5 divided by the total number of trees used for foraging by females at territory one without any restrictions on species, class or DBH class. Species, class and DBH class restrictions were used to avoid including trees that were for example, spruce, but not one of the dominant classes or DBH classes, as outlined previously. Similarly for foraging observation data, the same restrictions were used to generate the proportion of observations in each foraging zone and for each foraging technique for males and females at each territory. However, in this case the proportions were based on the total number of foraging observations not the total number of trees used for foraging. All foraging observation and tree characteristic variables, for each sex and random trees at each territory, were transformed to meet the assumptions of normality using a Freeman and Tukey transformation (Zarr 1996). This transformation is a modification of the arcsine square root transformation and is designed to yield better results for small and large proportions (i.e., near 0 and 1) (Zar 1996). Normality of all variables was examined using a Kolmogorov-Smirnov goodness of fit test (Zar 1996).

Previous studies that have examined foraging observations have pooled observations from different territories and individuals, artificially inflating the sample size and degrees of freedom. To avoid pseudoreplicating in this manner, I chose to analyze all foraging observation and tree characteristic data using repeated measures analysis of variance (RMA). I have defined the territory as my experimental unit and repeated measures (male, female and random observations) were carried out on each territory. The RMA design is the equivalent in an analysis of variance design to the paired t-test, in which multiple observations are made on the same experimental unit. However, when there are more than two treatment levels (in this case male, female and random) the RMA design is preferred since it allows a single hypothesis to be tested that there is no difference between treatments. I had expected more variability between territories than within territories and the repeated measures design protects for variability between units, in this case territories, allowing this variability to be eliminated from the experimental error (SPSS Inc. 1994).

All RMA analyses were performed using transformed variables. Species, burn class, DBH class, standing, foraging zone and foraging technique were included as within-subject factors. Tree (chosen by males, females or at random) was included as a between-subject factor in all analyses except certain tests involving the standing variable, where tree (standing trees used by males and females and random trees that were standing) was included as a within-subject factor. Within-subject factors distinguish between measurements (species, class, DBH class and standing) made on each unit (territory), whereas-between subject factors subdivide the unit into discrete groups, such as trees used by males and females and random trees (SPSS Inc. 1994).

Tree characteristic data were analysed using separate RMA analyses to examine differences between the proportions of standing trees, species, burn classes and DBH classes of trees used for foraging by males and females versus random trees and between males and females. In addition, I examined the interactions of standing trees, species and tree (chose by males, females or at random); class, species and tree; and DBH class, species and tree, in separate analyses. I was unable to examine all the higher order interactions (i.e. species by burn class by DBH class by tree) due to sample size limitations and the failure to meet the assumptions of normality required for the RMA

test. Differences in the proportions of foraging zones (ground, lower one-third, middle one-third and upper one-third of trees) and foraging techniques (pecking, scaling and excavating) used by male and female Black-backed woodpeckers were analyzed in separate RMA analyses. I also examined the interaction of foraging zone, species and sex. When the 3-way interaction was nonsignificant I examined the 2-way interaction of foraging zone and species.

Multivariate and univariate tests can be used to examine differences between within subject factors and interactions of within and between subject factors in the RMA design. Both tests assume normality, but the univariate test requires an additional assumption of sphericity, namely that the variances of differences for all treatment combinations be homogeneous. If these assumptions are met, especially for small sample sizes, the univariate approach is more powerful than the multivariate approach (Girden 1992). When conditions of sphericity were violated I used the Huynh-Feldt correction to the numerator and denominator degrees of freedom to validate the univariate F-statistic, allowing the more powerful univariate test to be used (Huynh and Feldt 1976). When the Huynh-Feldt correction was used the F-statistic was denoted as F_{HF} .

For analyses of tree characteristic data I used Tukey's post-hoc test following significant main effects to examine multiple comparisons of between subject factors with homogeneous variances and Games-Howell (GH) post-hoc tests when variances were heterogeneous (Zar 1996, Day and Quin 1989). I used estimated marginal means (EMMEANS), following significant main effects, to examine pairwise comparisons of sex in all analyses of foraging observation data. Post-Hoc tests were not possible with only 2 between subject factors (male and female). I also used EMMEANS to examine pairwise comparisons of within subject factors for both tree characteristic and foraging observation data. EMMEANS tests are based on the t-statistic formed by dividing the mean difference by the standard error and the degrees of freedom are based on the error term in the ANOVA table (Searle et al. 1980).

All RMA procedures were based on type III sums of squares. This procedure tests for the effect of an independent variable in the model on the dependent variable by adjusting for the effects of all other independent variables (SPSS Inc. 1997). In all analyses of foraging observation data and tree characteristic data I used an α -level of 0.10

to decrease the chance of committing a Type II error (Cohen 1988, Schmiegelow et al. 1997). Bonferroni adjustments (denoted as α_{BF}) were made to the specified α -level when multiple comparisons were used, except for Tukey Post Hoc tests and Games and Howell Post Hoc tests, which both protect for experiment wise error (Zar 1996, Day and Quin 1989). All statistical analyses were performed using SPSS (version 8.0).

3.2.5.2 Insect data

A Kolmogorov Smirnov goodness of fit test was used to examine the normality of all variables (Zar 1996). When data were normally distributed one-way ANOVA tests were used and when data were non-normal Kruskal-Wallis tests were used. Bark beetle biomass, wood-boring insect biomass, total insect biomass (bark beetle and wood-borers combined) and wood-boring insect gallery data were analysed separately to determine: 1) total differences between tree species for locations (basal, middle and top) combined; 2) differences between tree species for each location; and 3) differences between locations for tree species combined. Following a significant Kruskal-Wallis test, nonparametric Tukey multiple comparison tests were used to test for differences between locations (Zar 1996). In all analyses of insect data I used an α -level of 0.10 to decrease the chance of committing a Type II error (Cohen 1988). All analyses were performed using SPSS (version 8.0).

3.3 Results

3.3.1 Characteristics of trees used for foraging versus random trees and differences in the characteristics of trees used by males and females

Preliminary analyses indicated no differences between random trees associated with either males or females and therefore at the level of each territory, random trees were combined to create a single random tree classification for all future analyses.

Both males and females selected more jack pine and less spruce than expected by random foraging (RMA, $F = 4.59$, $p = 0.015$), although both tree species were used equally by both sexes (Figure 3.1). None of the burn classes were used differently than expected by random foraging (RMA, $F_{HF} = 0.20$, $p = 0.973$), but moderately burned trees were used more often and severely burned trees were used less often than the other burn classes (Figure 3.2). Males selected small diameter trees (36-75 mm) less and large diameter trees (151-250 mm and > 250 mm) more than expected by random (RMA, $F_{HF} =$

2.88, $p = 0.017$, Figure 3.3). However, medium (76-150 mm) and large diameter trees (151-250 mm) were used more than any of the other DBH classes of trees (Figure 3.3). The proportion of standing trees differed between trees used for foraging by males and females and random trees (RMA, $F = 2.894$, $p = 0.070$). However, no differences were detected by pairwise comparisons, although there was a trend for males to be using more standing trees (81.6%) than would have been expected by random (74.4%) (EMMEANS $\alpha_{BF} = 0.033$, $T = 2.14$, $p = 0.046$). Because the repeated measures analysis of variance is a more powerful test than the multiple comparison test, it is possible for the null hypothesis to be rejected and for the subsequent multiple comparison test to fail to detect any differences between any pairs of means (Zar 1996).

The interactions of species by burn class and species by DBH class revealed that both sexes selected moderately burned, large diameter (151-250 mm and > 250 mm) jack pine trees more and moderately burned, medium diameter (76-150 mm) spruce trees less than expected by random foraging (Table 3.1 and 3.2). However, only males selected large diameter (151-250 mm) jack pine trees for foraging more than spruce trees (EMMEANS, $T = 1.975$, $p = 0.055$). Females selected lightly burned jack pine and males selected heavily burned jack pine more than expected by random foraging (Table 3.1). The species effect was driving a significant interaction of species and standing trees used by males, females and randomly chosen standing trees (RMA, $F = 6.571$, $p = 0.003$). Standing spruce trees were selected less than expected by random (58.3%) by both sexes (35.2 % and 31.4 %) (Games Howell $\alpha = 0.10$, $T = 2.58$, $p = 0.010$ and $T = 3.05$, $p = 0.015$ respectively). Conversely, standing jack pine trees were selected more than random (16.1%) by both sexes (36.6 % and 50.2 %) (Games Howell $\alpha = 0.10$, $T = 2.04$, $p = 0.045$ and $T = 3.50$, $p = 0.005$ respectively).

Males and females did not differ in the proportions of either tree species, burn class, DBH class or standing trees used for foraging (Figures 3.1, 3.2 and 3.3). However, there was a trend for smaller trees (36-75mm) to be used more by females and larger trees (151-250mm) to be used more by males (RMA, $p = 0.112$ and $p = 0.175$ respectively, Figure 3.3).

3.3.2 Foraging zones and foraging techniques used by male and female black-backed woodpeckers

Males and females did not use different foraging zones or foraging techniques (RMA, $F_{HF} = 1.603$, $p = 0.207$ and $F_{HF} = 1.526$, $p = 0.226$ respectively, Figure 3.4 and 3.5). Both sexes foraged more on the lower one-third of trees than in either of the other 3 foraging zones and pecking was used more than either of the other 2 foraging techniques (Figure 3.4 and 3.5). The interaction of foraging zone, species and sex was not found to be significant (RMA, $F_{HF} = 1.553$, $p = 0.222$). However, the lower order interaction of foraging zone and species was significant (RMA, $F_{HF} = 6.219$, $p = 0.006$). Downed spruce trees (11.4 %) and the lower one-third of jack pine trees (44.8 %) were used more for foraging than downed jack pine trees (2.3%) and the lower one-third of spruce trees (19.9%) (EMMEANS $\alpha = 0.10$, $T = 2.18$, $p = 0.045$ and $T = 1.88$, $p = 0.078$ respectively).

3.3.3 Insect biomass and wood-boring insect gallery differences between tree species and locations

Bark beetle, wood-boring insect and total insect biomass (bark beetles and wood-borers combined) did not differ between spruce and jack pine trees when sampling locations on the tree were combined. However, there was a trend for greater total insect biomass in spruce than jack pine trees. The lower, middle and upper one-thirds of spruce and jack pine trees did not differ in either bark beetle or wood-boring insect biomass. Although, total insect biomass was higher in the lower one-third of spruce than jack pine trees, but middle and upper sections did not differ between tree species. When tree species were combined, both bark beetle and wood-boring insect biomass differed between locations, but no differences were found between location based on subsequent multiple comparison tests. However, total insect biomass was higher in the basal sections of trees than the middle and top sections (Table 3.3).

The total number of wood-boring insect galleries did not differ between spruce and jack pine trees, but there was a trend for more galleries in jack pine than spruce. Tree species did not differ with respect to the number of wood-boring insect galleries in the basal, middle and top sections. However, there was a trend showing more wood-boring insect activity in the basal section of jack pine trees than spruce. The number of insect

galleries was greater in the basal sections of trees than the middle and upper sections for tree species combined (Table 3.3).

3.4 Discussion

3.4.1 Foraging tree and foraging location selection

As predicted from previous studies Black-backed woodpeckers were using more conifer trees for foraging than any other tree species (Short 1974, Harris 1982, Goggans et al 1989, Villard and Beninger 1993, Villard 1994, Murphy and Lehnhausen 1998), although there were very few deciduous trees on any of the woodpecker foraging territories. However, I believe that this study is the first in the boreal region to demonstrate the selection of moderately burned large diameter jack pine and the lower one-third of jack pine trees for foraging in burned forests.

Wood-boring insects (Cerambycidae and Buprestidae) are the primary food source of Black-backed woodpeckers foraging in post-fire forests, although bark beetles (Scolytidae) are used to a lesser degree (Blackford 1955, Villard and Beninger 1993, Murphy and Lehnhausen 1998). In recently burned forests Black-backed woodpeckers focus their foraging efforts on the white-spotted sawyer larvae (*Monochamus scutellatus*), a long horned wood-borer (Villard and Beninger 1993, Murphy and Lehnhausen 1998). Larvae of this species can reach lengths of up to 50 mm and therefore represent a very substantial food item compared to the much smaller bark beetle larvae, which range from 5 to 7 mm depending on species (Ives and Wong 1988, Alberta Environmental Protection 1999).

The limiting factor for wood-boring insects and bark beetles post-fire is the moisture content of the wood; as trees dry out insect development and survival decreases (Richmond and Lejeune 1945, Werner and Post 1985). Moderately and heavily burned spruce desiccates within several months post-fire (see Richmond and Lejeune 1945). However, jack pine trees have thicker bark than spruce trees (Farrar 1995) and are less prone to bark peeling and desiccation both during the fire and when the trees remain standing post-fire (personal observation). Large DBH jack pine trees, due to their thicker bark (see Amman 1969), may be less prone to desiccation than small DBH trees and hence more suitable to wood-boring insects (see Cole and Amman 1969, Raske 1973). The lower one-third of jack pine trees is likely the area of the tree that retains the most

moisture post-fire due to the bark being thickest in this region of the tree (J. Hoyt personal observation). Furthermore, insects in the lower part of the tree would be insulated by the snow layer and also protected from woodpecker predation.

In this study I examined the selection of foraging habitat at two different scales: first, the selection of foraging trees at the level of the foraging territory and secondly the selection of locations within the trees, at the level of the trees used for foraging. At the level of the foraging territory, both sexes selected moderately burned, large diameter (151-250 mm and > 250 mm) and standing jack pine trees more and moderately burned, medium diameter (76-150 mm) and standing spruce trees less than expected by random foraging. At the level of the trees used for foraging, both sexes foraged on the lower one third of trees more than in any other foraging zones and the lower one third of jack pine trees were used more often than the lower one third of spruce trees. Therefore, I hypothesised that moderately burned large diameter jack pine trees and the lower one-third of jack pine trees retain moisture for a longer period post-fire than spruce trees and after 3-years post-fire they remain as suitable foraging substrates for wood-boring insects and hence Black-backed woodpeckers.

Insect data collected in the 3-year post-fire forest did not support this hypothesis. Due to sample size restrictions I was unable to examine insect biomass or wood-boring insect activity in relation to burn classes or DBH classes, therefore I am limited in my discussion to relationships between insects, tree species and foraging location. Contrary to my prediction, wood-boring insects were not more abundant in recently burned jack pine trees than spruce trees; only one spruce and one jack pine tree contained wood-boring insect larvae (*Monochamus spp.*). Furthermore, opposing trends were observed of higher total insect biomass in spruce trees and greater number of wood-boring insect galleries in jack pine. Insect data were not consistent with the foraging zones used by Black-backed woodpeckers on spruce and jack pine trees. Both sexes foraged primarily on the lower one-third of trees as expected by the higher biomass and greater number of galleries found in the basal sections of trees compared to the middle and top sections. However, both sexes used the lower one-third of jack pine trees for foraging more than spruce trees. Therefore, I expected wood-boring insect biomass and gallery measures to be higher in the basal sections of jack pine than spruce. However, this was not the case.

Furthermore, total insect biomass was higher in the basal sections of spruce and there was only a trend for more wood-boring insect activity in jack pine.

I believe these discrepancies are related to inadequacies in the insect sampling protocol. First, only 16 jack pine and 16 spruce trees were sampled and these came from one location within the burn and not from numerous woodpecker territories. Large fires, such as in this study, may dilute wood-boring insect attacks or result in pockets of trees throughout the burn sustaining light to severe attacks (Alberta Environmental Protection 1999). Second, sections taken from the base of the tree were 10 to 20 cm above the actual base. On jack pine, foraging was concentrated on the lower one-third of trees specifically within 0 to 10 cm of the ground and often on the roots, which is also where I observed the most successful foraging bouts (personal observation). On several occasions I extracted *Monochamus scutellatus* larvae from the roots and base of jack pine trees that were larger than larvae taken from the tree sections themselves, but I found no larvae in this region in spruce trees (see Appendix 3.2). Therefore, I believe that the lower 10 cm of jack pine trees was the area of highest insect abundance and also the large *Monochamus spp.* larvae in this region may represent the largest energy return per unit foraging effort. Third, discrepancies between wood-boring insect biomass and gallery measures existed within the data. Wood-boring insect larvae may have been present in the basal jack pine sections previously, but at the time of sampling they may have migrated lower in the tree leaving only their galleries. Gallery measures take into account insect activity pre-fire and also from immediately post-fire until I sampled at 3-years post-fire. Hence, it is possible to have similar gallery numbers between tree species, but the insects may have been present in the trees at different times.

Therefore, efforts to correlate foraging observations with the availability of wood boring insects and bark beetles in a 3-year post-fire forest should have included: 1) an insect sampling protocol designed to incorporate the very basal portion of the trunk, to represent where the birds were actually foraging; 2) sampling of a larger number of trees from a greater number of locations within the burn; and 3) an insect sampling protocol designed to test the hypothesis that the lower 0 to 10 cm of jack pine trees represented the area of highest wood-boring insect concentration in a 3-year-post-fire forest of spruce and jack pine mix. Future research could be designed to examine the hypothesis that the large

Monochamus spp larvae in the lower 0-10 cm of the tree represent the most profitable forage base and the largest energy return per unit foraging effort as compared to the smaller more easily accessible bark beetle larvae. These data would help to clarify foraging tree and foraging location selection data since it likely a combination of biomass and profitability that governs the selection of foraging trees and locations. Furthermore, sampling a larger number of trees of different burn classes and DBH classes would enable one to comment more accurately on the relationships between burn class, DBH and wood-boring insect and bark beetle infestation levels in post-burn forests.

In this study I did not sample insects in downed trees. Therefore I could not quantify why Black-backed woodpeckers foraged more on downed spruce trees than jack pine trees. However, downed spruce trees were more abundant than downed jack pine trees partly because spruce trees were more abundant than jack pine and also because they have a shallower root system (Farrar 1995) and are more prone to blow down post-fire than jack pine (personal observation). It is possible that downed spruce trees remain more suitable to wood-boring insects because they remain entirely below snow cover during the winter, thus retaining more moisture than standing trees.

Although spruce trees were selected for foraging less than expected by their availability on the foraging territories, both sexes used a considerable amount of burned spruce (females 46 % and males 39 %). Previous studies have shown that moderately burned spruce trees desiccate within several months post-fire (see Richmond and Lejeune 1945), therefore I did not expect Black-backed woodpeckers to forage as often on spruce as was observed. However, I found wood-boring insect larvae in moderately burned spruce trees 3 years after the fire. Therefore, spruce trees within my study area may not be as desiccated as expected and may still be able to maintain low level insect infestations.

Had this study been conducted immediately post-fire or during the first year post-fire I may have observed more foraging on moderately and heavily burned spruce trees. Immediately post-fire, wood-boring insects attack the more heavily burned trees and once these trees begin to desiccate the insects move into less severely burned trees (Richmond and Lejeune 1945). Murphy and Lehnhausen (1998) observed Black-backed woodpeckers foraging on less severely burnt substrates in the second year post-fire

compared to the first. I also observed old foraging scars on moderately and heavily burned spruce trees in our study area (personal observation). Furthermore had the study been conducted in closer proximity to the edge of the fire, where the burn severity was considerably less, I may have also observed more foraging on spruce trees that presumably would not have been subjected to as intense burning and hence desiccation.

3.4.2 Foraging tree and location differences between sexes

Pecking was the most prevalent foraging technique, but I expected to observe more excavating because Black-backed woodpeckers are known to be strong excavators (see Spring 1965, Murphy and Lehnhausen 1998). Pecking is used to extract beetle larvae from directly beneath the bark surface whereas excavating is the only viable technique for removing wood-boring larvae from beyond the cambium (see Villard and Beninger 1993, Villard 1994, Murphy and Lehnhausen 1998). I observed more bark beetle larvae 3 years post-fire than expected based on previous studies (see Richmond and Lejeune 1945, Werner and Post 1985, Murphy and Lehnhausen 1998). Therefore it is possible that within the 3-year post-burn forest of this study, bark beetle larvae represented a larger proportion of the diet of Black-backed woodpeckers than previously observed, providing a possible explanation for the observed increase in pecking. Furthermore, in my study, superficial strikes that removed small pieces of bark, but not wood chips were recorded as pecking. However, Murphy and Lehnhausen (1998) did not differentiate between superficial (to the cambium) and deeper excavating (to the sapwood). Therefore the superficial excavations observed in the previous study were likely recorded as pecking in our study, providing a possible explanation for the differences observed.

In this study I found no apparent partitioning of foraging trees, foraging locations or foraging behaviours by male and female Black-backed woodpeckers. The sexes did not differ with respect to the species, burn classes, DBH classes, standing trees, foraging zones and techniques used for foraging, although there was a trend for females to be selecting smaller trees and males larger trees. Both sexes used spruce and jack pine trees in equal proportions and moderately burned and medium and large diameter trees were used more than any of the other burn classes or DBH classes of trees and standing trees were used more by both sexes than downed trees. However, the results of previous

studies have been mixed with respect to foraging tree and behaviour partitioning between the sexes of *Picoides* species. Both Hairy (*Picoides villosus*) and Downy woodpeckers (*Picoides pubescens*) exhibit sexual differences in foraging niches (see Kilham 1965, 1970, Peters and Grubb 1983). However, Three-toed woodpeckers (*Picoides tridactylus*), the species most closely related to Black-backed woodpeckers, do not exhibit a defined foraging niche separation between the sexes during the spring and summer months (see Short 1974, Hogstad 1977, Villard 1994).

Murphy and Lehnhausen (1998) found that in recently burned forests male and female Black-backed woodpeckers differed in foraging height and in the burn classes of trees used for foraging, but in my study no such differences were observed during the spring and summer months. However, the study by Murphy and Lehnhausen involved sampling throughout the winter as opposed to my study which was confined to May and June. *Picoides* species that do not exhibit differences in foraging niche separation during the spring and summer months are known to partition resources during the winter months, primarily due to male dominance (see Hogstad 1976, 1991, Villard 1994). Therefore, it is possible that had my study been continued throughout the winter, the same pattern might have been observed. Alternatively, due to a high abundance of wood-boring insects and bark beetles in the recently burned forest (see Richmond and Lejeune 1945, Villard and Beninger 1993, Hutto 1995, Murphy and Lehnhausen 1998) it is possible that no partitioning would have taken place, but further research is needed to determine this.

No data were collected with respect to the horizontal partitioning of pairs during the breeding season (i.e. foraging in different areas of the territory), but I did observe males and females foraging in different locations within the foraging territory during the observational period (personal observation). Furthermore, I observed males displacing females on several occasions when foraging in close proximity to one another, but I also observed males and females foraging on the same tree without any such displacement. Again, further research would be needed to accurately comment on this observation.

3.4.3. Conclusions

The present study documents foraging tree and location selection as well as resource partitioning between the male and female Black-backed woodpeckers foraging

in a 3-year post-fire forest during May and June. Both sexes selected moderately burned large diameter standing jack pine trees for foraging more than expected if they had foraged at random. Furthermore, foraging was concentrated on the lower one-third of trees and on jack pine more so than spruce. Insect data collected within the 3-year post-fire forest was not consistent with the observed foraging tree and foraging location selection. Future coarse-scale insect sampling designed to quantify woodpecker foraging observations should sample a larger number of trees from a greater number of locations within the burned area. Furthermore, research should focus not only on insect biomass, but also on foraging profitability since it likely a combination of biomass and profitability that governs the selection of foraging trees and locations. A comparison of characteristics of trees used for foraging by male and female Black-backed woodpeckers indicated no apparent partitioning of resources between sexes during the summer months in a 3-year post-fire forest.

3.5 Literature Cited

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Table 3.1. Results of Post-Hoc tests (Games-Howell) (Repeated Measures ANOVA) for differences between the mean proportions of burn classes of tree species used for foraging by female and male Black-backed woodpeckers and versus what would have been expected by random foraging. Results are presented for spruce and jack pine trees separately. Mean proportions are based on proportions generated for each territory (N=17) for each of male, female and random trees. Mean proportions are presented as percentages with associated standard errors. Tests with significant p-values ($p < 0.10$) are presented in bold. Burn class 1: 1-80% burn, bark intact; Burn class 2: 100% burn, 80-100% bark intact; Burn class 3: 100% burn, 50-80% bark intact; Burn class 4: 100% burn 0-50% bark intact.

Species	Burn Class	Comparison	% + SE	Q Statistic	P - Value
Spruce	1	Female vs. Male	11.4 (3.1) vs. 14.3 (4.1)	0.478	0.882
		Female vs. Random	11.4 (3.1) vs. 14.3 (3.5)	0.374	0.919
		Male vs. Random	14.3 (4.1) vs. 14.3 (3.5)	0.103	0.995
	2	Female vs. Male	28.3 (5.2) vs. 20.5 (4.7)	1.43	0.431
		Female vs. Random	28.3 (5.2) vs. 41.7 (3.1)	2.08	0.074
		Male vs. Random	20.5 (4.7) vs. 41.7 (3.1)	3.52	0.003
	3	Female vs. Male	4.1 (1.3) vs. 3.6 (1.1)	0.091	0.996
		Female vs. Random	4.1 (1.3) vs. 6.5 (0.9)	1.56	0.267
		Male vs. Random	3.6 (1.1) vs. 6.5 (0.9)	1.65	0.166
	4	Female vs. Male	1.9 (0.8) vs. 1.3 (0.6)	0.614	0.840
		Female vs. Random	1.9 (0.8) vs. 2.9 (0.5)	0.558	0.844
		Male vs. Random	1.3 (0.6) vs. 2.9 (0.5)	1.17	0.423
Jack Pine	1	Female vs. Male	6.7 (2.4) vs. 2.9 (1.2)	1.43	0.410
		Female vs. Random	6.7 (2.4) vs. 2.2 (0.8)	2.35	0.085
		Male vs. Random	2.9 (1.2) vs. 2.2 (0.8)	0.926	0.494
	2	Female vs. Male	23.5 (5.0) vs. 35.8 (6.3)	1.56	0.373
		Female vs. Random	23.5 (5.0) vs. 10.1 (2.0)	1.87	0.087
		Male vs. Random	35.8 (6.3) vs. 10.1 (2.0)	3.46	0.005
	3	Female vs. Male	7.6 (2.4) vs. 8.7 (2.5)	0.597	0.867
		Female vs. Random	7.6 (2.4) vs. 2.8 (0.7)	1.86	0.136
		Male vs. Random	8.7 (2.5) vs. 2.8 (0.7)	2.47	0.028
	4	Female vs. Male	1.6 (0.7) vs. 2.8 (1.2)	0.823	0.723
		Female vs. Random	1.6 (0.7) vs. 2.0 (0.6)	0.347	0.914
		Male vs. Random	2.8 (1.2) vs. 2.0 (0.6)	1.17	0.508

Table 3.2. Results of Post-Hoc tests (Games-Howell) (Repeated Measures ANOVA) for differences between DBH classes of tree species used for foraging by female and male Black-backed woodpeckers and versus what would have been expected by random. Results are presented for spruce and jack pine trees separately. Mean proportions are based on proportions generated for each territory (N=17) for each of male, female and random. Mean proportions are presented as percentages with associated standard errors. Tests with significant p-values ($p < 0.10$) are presented in bold. DBH class 1 was not used in analyses due to extremely low proportions used and available (<4%). DBH class 2: 36 - 75 mm; DBH class 3: 76-150 mm; DBH class 4: 151-250 mm; DBH class 5 > 250 mm.

Species	DBH Class	Comparison	% + SE	Q Statistic	P - Value
Spruce	2	Female vs. Male	8.2 (2.4) vs. 3.3 (1.6)	1.74	0.247
		Female vs. Random	8.2 (2.4) vs. 12.3 (2.0)	1.62	0.280
		Male vs. Random	3.3 (1.6) vs. 12.3 (2.0)	3.36	0.001
	3	Female vs. Male	23.4 (3.3) vs. 12.9 (3.1)	2.53	0.074
		Female vs. Random	23.4 (3.3) vs. 33.8 (2.5)	2.15	0.069
		Male vs. Random	12.9 (3.1) vs. 33.8 (2.5)	4.68	> 0.001
	4	Female vs. Male	10.4 (2.4) vs. 12.5 (3.6)	0.107	0.995
		Female vs. Random	10.4 (2.4) vs. 15.1 (1.9)	1.205	0.311
		Male vs. Random	12.5 (3.6) vs. 15.1 (1.9)	1.10	0.547
	5	Female vs. Male	3.5 (1.8) vs. 10.9 (5.7)	1.37	0.458
		Female vs. Random	3.5 (1.8) vs. 4.3 (1.8)	0.04	0.998
		Male vs. Random	10.9 (5.7) vs. 4.3 (1.8)	1.41	0.442
Jack Pine	2	Female vs. Male	1.2 (0.8) vs. 0.4 (0.3)	0.672	0.749
		Female vs. Random	1.2 (0.8) vs. 1.0 (0.7)	1.92	0.230
		Male vs. Random	0.4 (0.3) vs. 1.0 (0.7)	1.26	0.379
	3	Female vs. Male	17.9 (5.2) vs. 21.9 (6.9)	0.487	0.906
		Female vs. Random	17.9 (5.2) vs. 8.9 (2.2)	1.17	0.356
		Male vs. Random	21.9 (6.9) vs. 8.9 (2.2)	1.66	0.225
	4	Female vs. Male	14.3 (3.4) vs. 22.9 (5.2)	1.51	0.410
		Female vs. Random	14.3 (3.4) vs. 6.2 (1.1)	1.81	0.082
		Male vs. Random	22.9 (5.2) vs. 6.2 (1.1)	3.33	0.009
	5	Female vs. Male	6.0 (3.8) vs. 5.0 (1.8)	0.087	0.997
		Female vs. Random	6.0 (3.8) vs. 1.0 (0.5)	2.30	0.087
		Male vs. Random	5.0 (1.8) vs. 1.0 (0.5)	2.39	0.011

Table 3.3 Results of analyses of bark beetle biomass (BB), wood-boring insect biomass (WB), total insect biomass (TOT) and wood-boring insect hole (WBH) data collected in a 3-year post-fire forest to test for differences between tree species for sampling locations on the tree combined, differences between tree species for sampling locations on the tree separately and differences between tree species for sampling location on the tree combined. A total of 16 spruce and 16 jack pine trees were sampled. Kruskal Wallis tests (K-W) were based on the Chi-square statistic. The analysis of variance test (ANOVA) was based on the F statistic and Tukey multiple comparisons tests were based on the Q statistic ($Q_{0.10, \infty, 3}$). Biomass measures (Mean \pm SE) represent milligrams (mg) and wood-borer holes (Mean \pm SE) represent the number of holes. Significant relationships ($p < 0.10$) are shown in bold.

Description	Analysis	Data	Mean \pm SE	Test	Statistic	P-Value
Differences between tree species for sampling locations combined	Spruce vs. Jack pine	BB	0.2(0.1) vs. 2.3(1.1)	K-W	1.02	0.31
		WB	12.9(12.9) vs. 3.1(2.3)	K-W	1.72	0.19
		TOT	13.1(12.8) vs. 5.3(2.4)	K-W	2.30	0.13
		WBH	2.6(1.1) vs. 6.6(2.3)	Anova	2.58	0.12
Differences between tree species for locations separately	Basal sections	BB	0.2(0.1) vs. 2.2(1.1)	K-W	1.84	0.18
	Spruce vs. Jack pine	WB	12.9(12.9) vs. 3.1(2.3)	K-W	1.72	0.19
		TOT	13.0(12.8) vs. 5.3(2.4)	K-W	3.24	0.07
		WBH	12.2(1.1) vs. 5.6(2.2)	K-W	2.54	0.11
Middle sections	BB	0.0(0.0) vs. 0.0(0.0)	K-W	0.00	1.00	
Spruce vs. Jack pine	WB	0.0(0.0) vs. 0.0(0.0)	K-W	0.00	1.00	
	TOT	0.0(0.0) vs. 0.0(0.0)	K-W	0.00	1.00	
	WBH	0.3(0.3) vs. 0.7(0.4)	K-W	1.80	0.18	
Upper sections	BB	0.08(0.08) vs. 0.04(0.04)	K-W	0.002	0.96	
Spruce vs. Jack pine	WB	0.0(0.0) vs. 0.0(0.0)	K-W	0.00	1.00	
	TOT	0.08(0.08) vs. 0.04(0.04)	K-W	0.002	0.96	
	WBH	0.0(0.0) vs. 0.4(0.3)	K-W	2.06	0.15	

Differences between locations for tree species combined	Basal vs. middle vs. upper	BB WB TOT WBH	1.2(0.6) vs. 0.0(0.0) 8.0(6.5) vs. 0.0(0.0) 9.2(6.5) vs. 0.0(0.0) 3.9(1.2) vs. 0.5(0.2)	K-W K-W K-W K-W	13.73 10.43 20.56 17.41	<0.01 <0.01 <0.01 <0.01
Post-Hoc multiple comparisons for differences between locations for tree species combined						
Basal vs. middle	BB WB TOT WBH	1.2(0.6) vs. 0.0(0.0) 8.0(6.5) vs. 0.0(0.0) 9.2(6.5) vs. 0.0(0.0) 3.9(1.2) vs. 0.5(0.2)	Tukey Tukey Tukey Tukey	2.75 1.52 3.76 3.24	>0.10 >0.10 <0.10 <0.10	
Basal vs. upper	BB WB TOT WBH	1.2(0.6) vs. 0.06(0.04) 8.0(6.5) vs. 0.0(0.0) 9.2(6.5) vs. 0.06(0.04) 3.9(1.2) vs. 0.2(0.2)	Tukey Tukey Tukey Tukey	2.16 1.52 3.43 4.12	>0.10 >0.10 <0.10 <0.10	
Middle vs. upper	BB WB TOT WBH	0.0(0.0) vs. 0.06(0.04) 0.0(0.0) vs. 0.0(0.0) 0.0(0.0) vs. 0.06(0.04) 0.5(0.2) vs. 0.2(0.2)	Tukey Tukey Tukey Tukey	0.60 0.00 0.59 0.87	>0.10 >0.10 >0.10 >0.10	

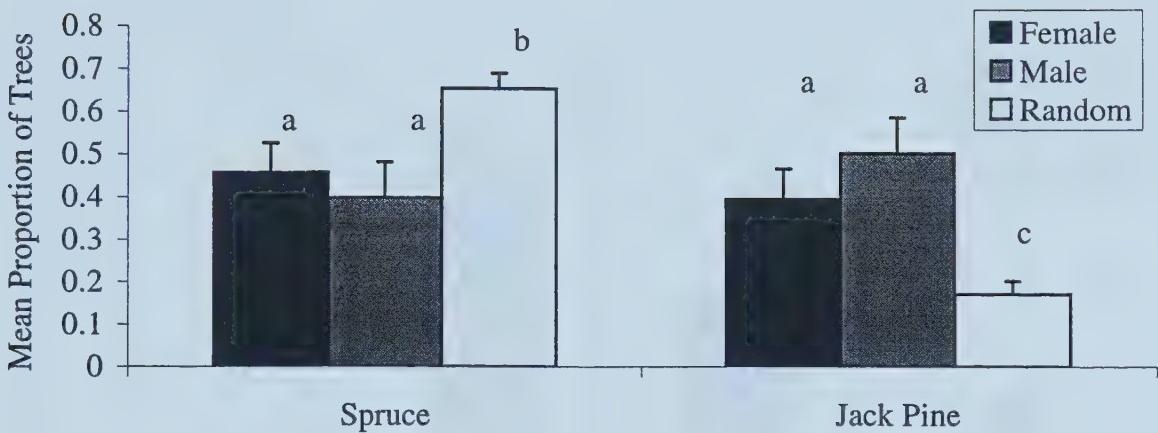


Figure 3.1. Mean (+ SE) proportions of spruce and jack pine trees used for foraging by female and male Black-backed woodpeckers and as expected by random foraging. Proportions were generated for each territory (N=17) for each male, female and random trees. Statistically significant differences ($p<0.10$, Games-Howell) between males and females and random trees are shown by a difference of one letter or greater.

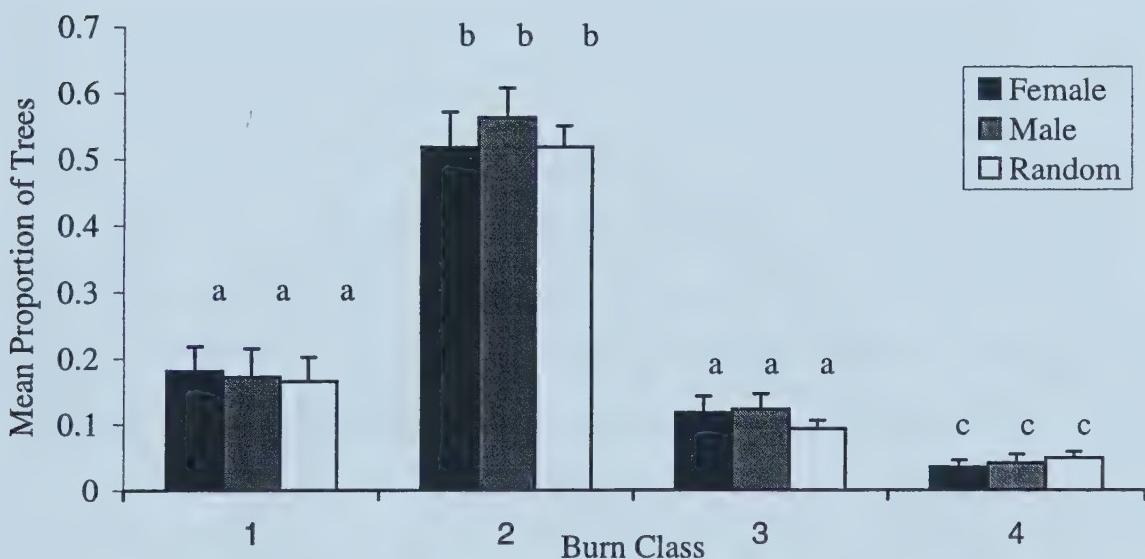


Figure 3.2. Mean (+ SE) proportion of burn classes used for foraging by male and female Black-backed woodpeckers and as expected by random foraging. Proportions were generated for each territory (N = 17) for each male, female and random trees. Statistically significant differences ($p<0.017$, EMMEANS) between burn classes of trees used for foraging by females and males are shown by a difference of one letter or greater. Bonferroni adjustments were made to α ($0.10/6 = 0.017$) based on 6 multiple comparisons. Burn class 1: 1-80% burn, bark intact; Burn class 2: 100% burn, 80-100% bark intact; Burn class 3: 100% burn, 50-80% bark intact; Burn class 4: 100% burn 0-50% bark intact.

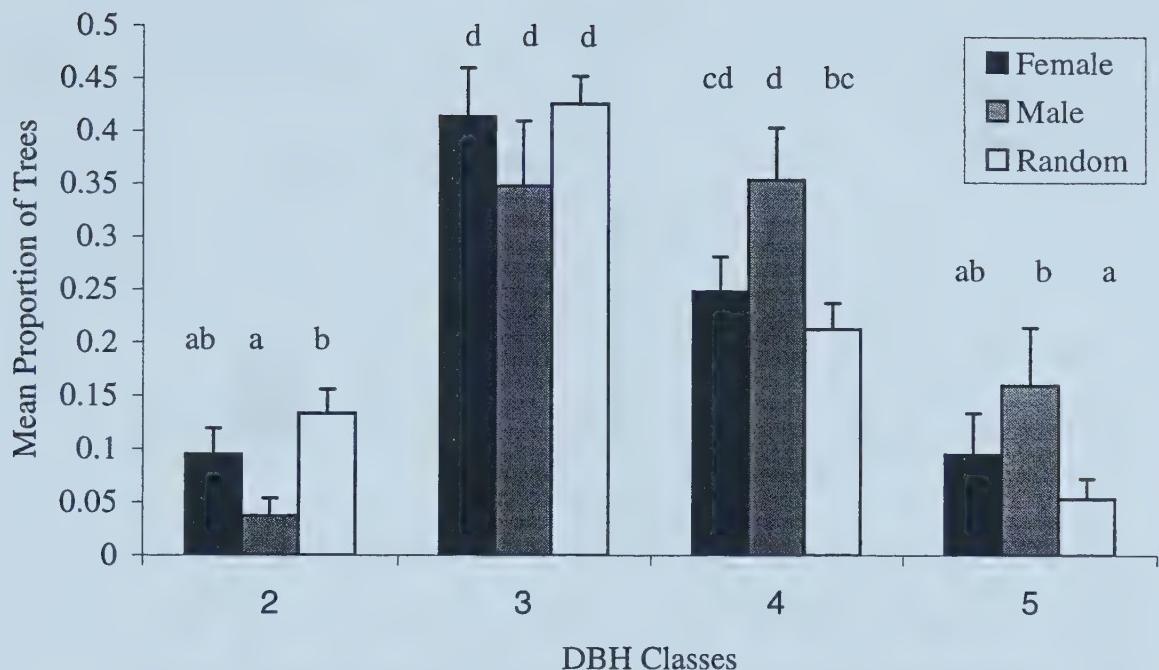


Figure 3.3. Mean (+ SE) proportion of DBH classes used for foraging by male and female Black-backed woodpeckers and as expected by random foraging. Proportions were generated for each territory ($N=17$) for each male, female and random trees. DBH class 1 was not used in analyses due to extremely low proportions used and available (<4%). Statistically significant differences ($p<0.10$, Tukey) between female, male and random trees and statistically significant differences ($P<0.017$, EMMEANS) within each sex with respect to DBH classes used for foraging, are both shown by a difference of one letter or greater. Bonferroni corrections were made to the specified α level of 0.10 for within sex comparisons of DBH classes (EMMEANS) based on the 6 multiple comparisons conducted ($0.10/6 = 0.017$). DBH class 2: 36 - 75 mm; DBH class 3: 76-150 mm; DBH class 4: 151-250 mm; DBH class 5 > 250 mm.

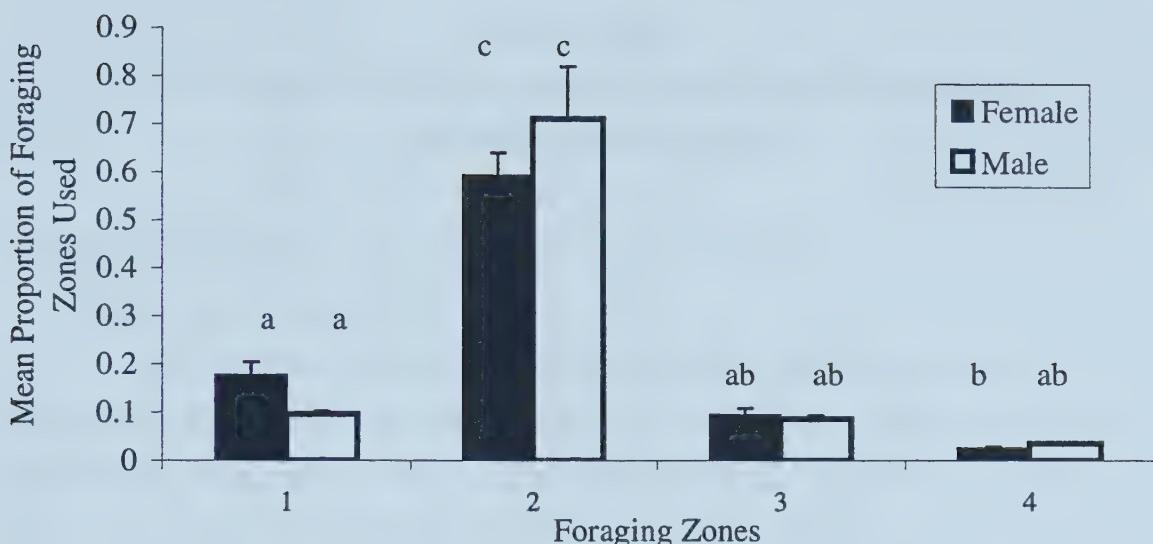


Figure 3.4. Mean (+ SE) proportion of foraging zones used by male and female Black backed woodpeckers. Proportions were generated for each territory (N=17) for each male and female. Statistically significant differences ($P<0.017$, EMMEANS) between foraging zones used by females and also by males, are shown by a difference of one letter or greater. Bonferroni corrections were made to the specified α level based on 6 multiple comparisons conducted ($0.10/6 = 0.017$). Zone 1: downed trees; Zone 2: lower 1/3 of tree; Zone 3: middle 1/3 of tree; Zone 4: upper 1/3 of tree.

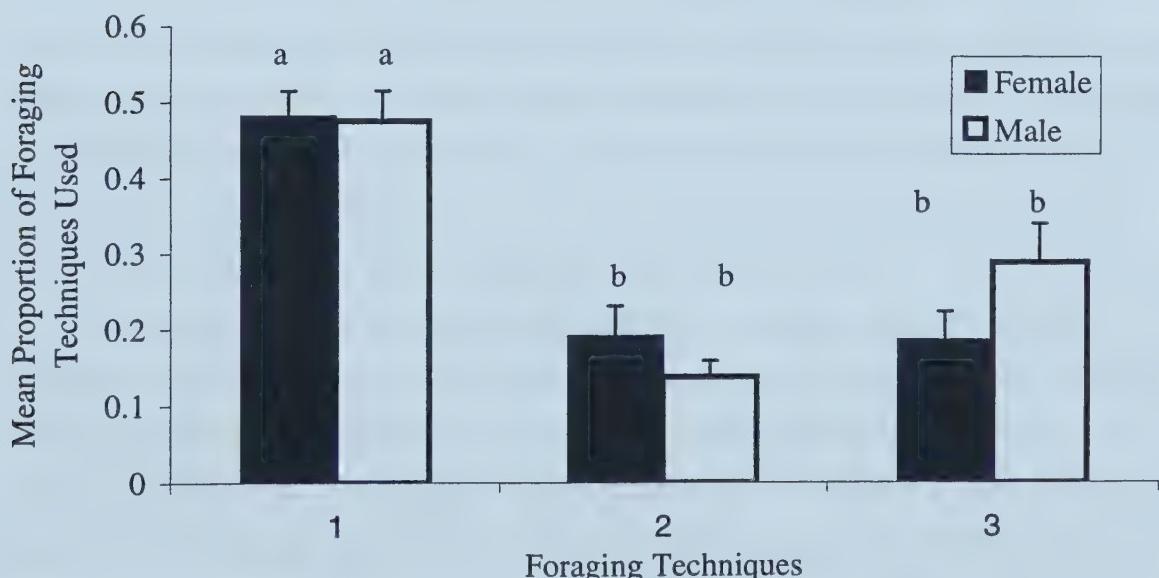


Figure 3.5. Mean (+ SE) proportion of foraging techniques used by male and female Black-backed woodpeckers. Proportions were generated for each territory (N=17) for each male and female. Statistically significant differences ($p<0.033$, EMMEANS) between foraging techniques used by females and also by males are shown by a difference of one letter or greater. Bonferroni corrections were made to the specified α level based on the 3 multiple comparisons that were conducted ($0.10/3 = 0.033$). Technique 1: pecking; Technique 2: scaling; Technique 3: excavating.

CHAPTER 4

CONCLUSIONS, MANAGEMENT RECOMMENDATIONS AND FUTURE RESEARCH

4.1 Recommendations for management of post-fire forests

4.1.1 *Black-backed woodpeckers*

In 1997 and 1998, representing 2 and 3 years post-fire, Black-backed woodpeckers were equally likely to occur in burned white spruce, black spruce and jack pine habitats. I was unable to predict Black-backed presence or absence in recently burned forests based on vegetation characteristics. However, 95% of the trees used for foraging by Black-backed woodpeckers in the 3 year post-fire forest were greater than 147 mm DBH and both sexes selected moderately burned, large diameter and standing jack pine trees for foraging more than expected if they had foraged at random. I found no apparent partitioning of foraging trees, foraging locations or foraging behaviors by male and female Black-backed woodpeckers.

I was unable to examine the density of trees used for foraging. However, black spruce and jack pine sites, where Black-backs were detected during surveys, had a mean density of trees greater than 147 mm DBH and standing dead trees of (mean \pm SE) 13.0 \pm 1.7 and 38.1 \pm 2.1 / 100 m² respectively. At white spruce sites where birds were detected, the mean density of trees greater than 147 mm and standing dead trees were 24.4 \pm 4.9 and 31.3 \pm 4.0 / 100 m² respectively (see Appendix 2.1).

Although I did not observe any differences in occurrence of Black-backed woodpeckers between white spruce, black spruce and jack pine dominated habitats during habitat association surveys, birds in the spruce dominated habitats were probably selecting jack pine trees for foraging. Had this study been conducted immediately post-fire or at a different time of the year, differences in foraging tree selection may have been observed and possibly differences between the sexes (see Hogstad 1977, 1978, Murphy and Lehnhausen 1998). Immediately post-fire spruce trees probably represent a more suitable foraging substrate since they die faster and are attacked by insects sooner, but as a result become desiccated sooner than jack pine trees (Richmond and Lejeune 1945).

In post-fire forests aged 3, 4 and 8 years, Black-backed woodpecker presence was best predicted by the proportion of trees that were 100% burned with 0-50% bark intact. However, the majority of presences that were correctly predicted were from the 8 year post-fire forests. As trees age post-fire, the bark begins to peel, therefore after 8 years post-fire trees with 0-50% bark remaining likely had greater than 80% bark remaining immediately post-fire.

Therefore, I recommend that in areas of mixed spruce and jack pine, salvage logging operations should be designed to leave an equal amount of standing dead spruce and jack pine trees at a density of $38.1 \pm 2.1 / 100 \text{ m}^2$. These areas should contain trees greater than 147 mm DBH at densities of $13.1 \pm 3.1 / 100 \text{ m}^2$ or greater. In white spruce dominated areas, leave areas should contain densities of standing dead trees of $31.3 \pm 4.0 / 100\text{m}^2$, where trees greater than 147 mm exceed densities of $24.4 \pm 4.9 / 100 \text{ m}^2$. These density measurements were made at 3 years post-fire and therefore should be treated as minimum values since tree density may have been higher immediately post-fire when salvage logging operations would normally occur. Trees in leave areas should be lightly to moderately burned with a high degree of bark retention and not simply the severely burned trees that are of no economic value. This will also help to ensure that trees with up to 50% bark retention will be present in 8 year post-fire forests. The minimum nest tree requirement of Black-backed woodpeckers in the 3 year post-fire forests was 181 mm and there did not appear to be any selection for tree species or degree of burn (see Appendix 3.1). Therefore, leave areas should also be designed to include areas where tree DBH exceeds 181 mm, but I cannot comment on the density of trees required.

4.1.2. Three-toed woodpeckers

Based on the results of this study managing for Black-backed woodpecker habitat in post-fire forests may not fulfill the habitat requirements of Three-toed woodpeckers. Similar to Black-backed woodpeckers, Three-toed woodpecker occurrence did not differ between burned white spruce, black spruce and jack pine habitats. However, Three-toed presence in the 3 year post-fire forests was negatively associated with the density of heavily burned and jack pine trees. At sites where Three-toed woodpeckers were detected, the mean density of heavily burned and jack pine trees was (mean \pm SE) 5.4 ± 1.4 and $4.5 \pm 1.8 / 100 \text{ m}^2$ respectively. In different aged post-fire forests Three-toed

presence was negatively associated with the density of moderately burned and jack pine trees and positively associated with the density of lightly burned trees. At sites where Three-toed woodpeckers were detected, the mean density of moderately burned, jack pine and lightly burned trees was (mean \pm SE) 21.8 ± 4.1 , 3.6 ± 1.3 and $21.5 \pm 10.7 / 100 \text{ m}^2$, respectively.

Therefore, managing for Three-toed woodpeckers in post-fire forests will require leaving areas of lightly burned spruce trees, where the density of heavily burned (100% burn, 0-80% bark intact) and jack pine trees should not exceed 5.4 ± 1.4 and $4.5 \pm 1.8 / 100 \text{ m}^2$ respectively. In black spruce and jack pine dominated stands the density of standing dead trees should be (mean \pm SE) $39.8 \pm 2.9 / 100 \text{ m}^2$ and in white spruce dominated stands, $28.5 \pm 3.9 / 100 \text{ m}^2$. Areas of lightly burned spruce are most likely to be in conflict with salvage logging operations since lightly burned trees are easier to process than severely burned trees (Werner and Post 1985). I was unable to provide recommendations with respect to the DBH of trees used for foraging or nesting for Three-toed woodpeckers, but as a general rule until further research can be conducted, the same DBH ranges and densities specified for Black-backed woodpeckers could be used. These values are consistent with the DBH ranges reported by previous studies (see Villard 1999, Murphy and Lehnhausen 1998).

4.1.3 Size requirements of Black-backed and Three-toed woodpeckers

I did not specifically look at size or area requirements of either woodpecker species in recently burned forests, but I found pairs spaced approximately 500 m apart 2 and 3 years post-fire, which would be equal to a territory size of approximately 25 ha. Murphy and Lehnhausen (1998) found that for a period up to 2 years post fire, densities of both species were approximately 0.2/ha, which translates into approximately 20 ha / pair. However, it is not clear if area requirements increase with years post-fire due to possible decreases in insect abundance. Furthermore area requirements might increase during the winter months or while feeding juveniles (see Goggans et al. 1989). Hence, 20 and 25 ha are probably underestimates of the area required by a single pair of Black-backed or Three-toed woodpeckers and 40 ha would likely serve as a cautious estimate for the woodpeckers. Therefore, leave areas should be designed to be as large or larger than 40 ha, containing the densities of trees outlined previously for both species.

However, the absolute area required will depend on how many pairs are required to ensure population persistence through time. This is a much more difficult question to address and one that is beyond the scope of this project or any in the near future. Therefore, best guess estimates must be made with respect to the size of burns that should be salvaged as well as how much of the burn should be salvaged. I will address these points briefly in the following section on salvage logging.

4.1.4 *The role of salvage logging*

In recent years there has been an increasing trend towards forest management that emulates natural disturbance (Alberta Pacific 1992, Hunter 1993, Volney et. al 1999). Fire is the dominant natural disturbance in the boreal region (Rowe and Scotter 1973) and a great deal of work has been done to examine the patterns and processes of fire on the landscape (Haila et al. 1994, Gauthier et al. 1996, Armstrong et al. 1999, Weir et al. 1999). However, the role and value of standing dead trees post-fire continues to be undervalued (see Hutto 1995). For example, when a forest fire occurs the first reaction of the government and the forest industry has been to access an area as soon as possible and salvage any “economically viable timber”. Public perception that stand replacing fires are catastrophic and destructive (see Biswell 1968, Alexander and Dube 1982), perpetuate the problem of salvage logging. As a result there are very few regulations within the province of Alberta that govern timber harvesting in recently burned forests.

One of the major operational constraints of salvage logging is time. Recently burned trees must be harvested before they desiccate and split and also before wood-boring insect galleries become too extensive. This represents an absolute maximum of 2 years post-fire for saw logs and possibly slightly longer for lower quality wood products (personal communication J. Russell, Millar Western Forest Products). Therefore, in extremely large burns, such as the Mariana Lake burn at 135,000 ha, salvage logging may not be as much of a concern since only a small percentage of the burned area generally can be salvaged prior to desiccation and beetle activity. Furthermore, since these large burns generally include a large proportion of non-commercially viable timber (i.e. black spruce and mixed black spruce and jack pine) (S. Cumming, personal communication) there is generally a large amount of burned habitat remaining after salvage logging of commercially viable timber (J. Hoyt, personal observation). However, salvage logging

and habitat loss becomes much more of a concern in smaller burns (eg. < 2000 ha), which can be logged within time constraints, thus leaving only a small amount of suitable recently burned habitat. Furthermore, for species that appear to be closely associated with recently burned forests these small fires likely represent “stepping stones” between large patches of suitable recently burned habitat (see also Hutto 1995, Murphy and Lehnhasuen 1998).

Therefore, I feel that the practice of salvage logging, particularly in smaller burned areas, needs to be immediately re-evaluated. There is no reason why the loss of recently burned habitat should be treated any differently than the loss of any other habitat type on the landscape. Clearly what are needed, are more detailed regulations governing the size and species of trees that can be salvaged as well as the size and configuration of harvest and leave patches. Unfortunately, all of the data needed to formulate these regulations are not currently available. However, I believe that by managing for the habitat requirements of Black-backed and Three-toed woodpeckers in post-fire forests potentially the requirements of other species that use recently burned forests may be met. For example; Hairy woodpeckers *Picoides villosus*, Downy woodpeckers *Picoides pubescens*, Northern flickers *Colaptes auritus*, Mountain bluebirds *Sialia currucoides*, House wrens *Troglodytes aedon*, Northern Hawk Owls *Surnia ulula*, American Kestrels *Falco sparverius* and numerous other secondary cavity nesters (see Blackford 1955, Taylor and Barmore Jr. 1980, Apfelbaum and Haney 1981, Harris 1982, Hutto 1995, Caton 1996, Hoffman 1997). However, the habitat requirements of these species may differ substantially from those of Black-backed and Three-toed woodpeckers. Therefore, management of post-fire forests will require addressing the habitat requirements of other species’ as these data become available.

As a starting point, I believe that salvage logging of areas less than 2000 ha should be stopped until further research can be done to determine the role of these smaller burns in the population dynamics of species that appear to be closely associated with recently burned forests. Furthermore, at no point should more than 50% of available Black-backed and Three-toed woodpecker habitat be salvage logged. Although these numbers may seem arbitrary, and will definitely need to be clarified in future

studies, they should serve as cautionary measures to mitigate the effects of habitat loss until further studies can be conducted.

This approach could be developed into an adaptive management framework (see Walters 1986, Schmiegelow and Hannon 1993) whereby researchers, industry and government representatives work to develop salvage logging techniques and regulations. For example, developing techniques and cut patterns that attempt to find threshold densities of standing dead trees that result in woodpecker densities similar to those in non-salvage logged areas. Another option would be to conduct cost-benefit analyses of the various management options that include both ecological and economical variables.

Complicating the effects of salvage logging are the effects of fire suppression. When ignitions are temporally separated and drying conditions are not extreme, fire suppression is an effective tool (see Cumming 1997) and there are probably fewer fires in any size class, above a few hectares, than used to be the case (S. Cumming, personal communication). Therefore, if the future trend is for increased fire suppression forest managers may have to address the possibility of prescribed burning.

4.2 Recommendations for management of unburned forests

4.2.1 *Black-backed woodpeckers*

Black-backed woodpeckers were initially not detected in unburned forests within 50 km of a recently burned forest, but they were detected in unburned coniferous forests further away from recently burned forests. Their occurrence was highest in old growth black spruce forests and presence at these sites was positively associated with the density of standing and deciduous trees and mean DBH. Old black spruce sites occupied by Black-backs had a mean density of deciduous and standing trees of (mean \pm SE) 3.0 ± 1.4 and $60.3 \pm 6.2/100\text{ m}^2$ respectively and a mean DBH of 162.0 ± 19.3 . Although black spruce is often considered to be nonmerchantable there are several companies in the province of Alberta that harvest black spruce. Therefore, the DBH measures and density of standing trees mentioned above could be used at the stand level to manage for Black-backed woodpeckers in black spruce forests. Furthermore, there have been rumors of “fire proofing” the landscape, by creating large cuts in black spruce areas to act as fire breaks between the lowland black spruce areas, where the majority of fires start, and upland mixedwood forests. Still it is unclear as to how important these old growth black

spruce forests are in the population dynamics of Black-backed woodpeckers. Therefore, until future research efforts can address the source-sink dynamics of black-backed woodpeckers in recently burned forests and old growth black spruce forests, I recommend that both habitats be considered important and treated equally in management efforts.

4.2.2 Three-toed woodpeckers

Based on stand ages obtained from Phase 3 Forest Inventory data (Alberta Forestry, Lands and Wildlife 1985), Three-toed woodpeckers were detected in old and mature coniferous forests and there was no difference in occupancy of white spruce, black spruce and jack pine. However, based on vegetation characteristics collected at each site, a DFA classified sites differently than Phase 3 data. The mature white spruce and jack pine site where I had detected Three-toed woodpeckers had vegetation characteristics that resembled more closely old growth than mature sites. A reanalysis of occupancy data with these revised classifications revealed that they occupied only old growth and not mature coniferous forests. Therefore, I do not recommend that Phase 3 Forest Inventory maps and associated stand ages be used to manage for Three-toed woodpeckers in unburned forests. Instead I believe that management should be based on structural characteristics not stand age. I have summarized the vegetation characteristics of unburned sites where Three-toed woodpeckers were detected in Appendix 2.1., which can be used at the stand level to predict suitable Three-toed woodpecker habitat. If in certain circumstances stand ages must be used for management purposes I recommend that unburned white spruce, black spruce and jack pine stands older than 110 years be managed for Three-toed woodpecker habitat.

4.3 Recommendations for future research

A more extensive insect sampling protocol is needed to provide more information about the tree characteristics that contain the highest densities of bark beetle and wood-boring insects. Future efforts should include: 1) an insect sampling protocol designed to incorporate the very basal portion of the trunk in recently burned forests, to represent where the birds were actually foraging; 2) sampling of a larger number of trees of varying DBH, decay and burn classes to examine relationships between DBH, decay class, burn class and wood-boring insect and bark beetle infestation levels and; 3) sampling of a

larger number of trees from a greater number of locations within burned and unburned forests. This would improve one's ability to predict which vegetation characteristics are most likely to be related to woodpecker presence or absence. However, future research should focus not only on insect biomass, but foraging profitability (i.e. the size of food items, where they are concentrated and the energy return per unit foraging effort), since it is likely a combination of biomass and profitability that governs the selection of foraging trees and locations.

I was unable to examine the size requirements of Three-toed woodpeckers in old growth forests, but information from elsewhere suggests that territories may be as large as 1 km² (Klenner and Huggard 1997) and equally as large if not larger for Black-backed woodpeckers (Goggans et al. 1989). Therefore, management for these two species will require leaving large tracts of old growth coniferous forests greater than 1 km². However, how large to make these areas will depend on how large a population is needed, which requires further research into the population dynamics of both woodpecker species. Furthermore, questions still remain with respect to the distribution of these patches. For example, do patches of old growth embedded in a matrix of mature forests represent suitable habitat or are old growth patches that are adjacent to old black spruce more suitable than those adjacent to old jack pine? To answer these questions a more detailed landscape level approach is required that examines attributes of patch size and adjacency.

There are several areas that require further research before the population dynamics of Black-backed woodpeckers can be fully understood. The most important of which is determining the source-sink dynamics (see Pulliam and Danielson 1991) of Black-backed woodpeckers in recently burned forests and old growth black spruce forests. In addition, for future modeling exercises it would also be useful to determine at any one point in time what proportion of the landscape was old growth black spruce versus recently burned forests (0-8 years). These data would provide an indication as to which type of habitat contains the most Black-backed woodpeckers at any one time and whether there are prolonged periods where recently burned forests are absent from the landscape. Furthermore, a detailed examination is needed of the relationships between fire size, frequency of fire, distance to other recently burned areas and Black-backed

woodpecker dispersal abilities. Answering these questions will also enable one to comment more accurately on the effects of salvage logging and fire suppression on the population dynamics of Black-backed woodpeckers.

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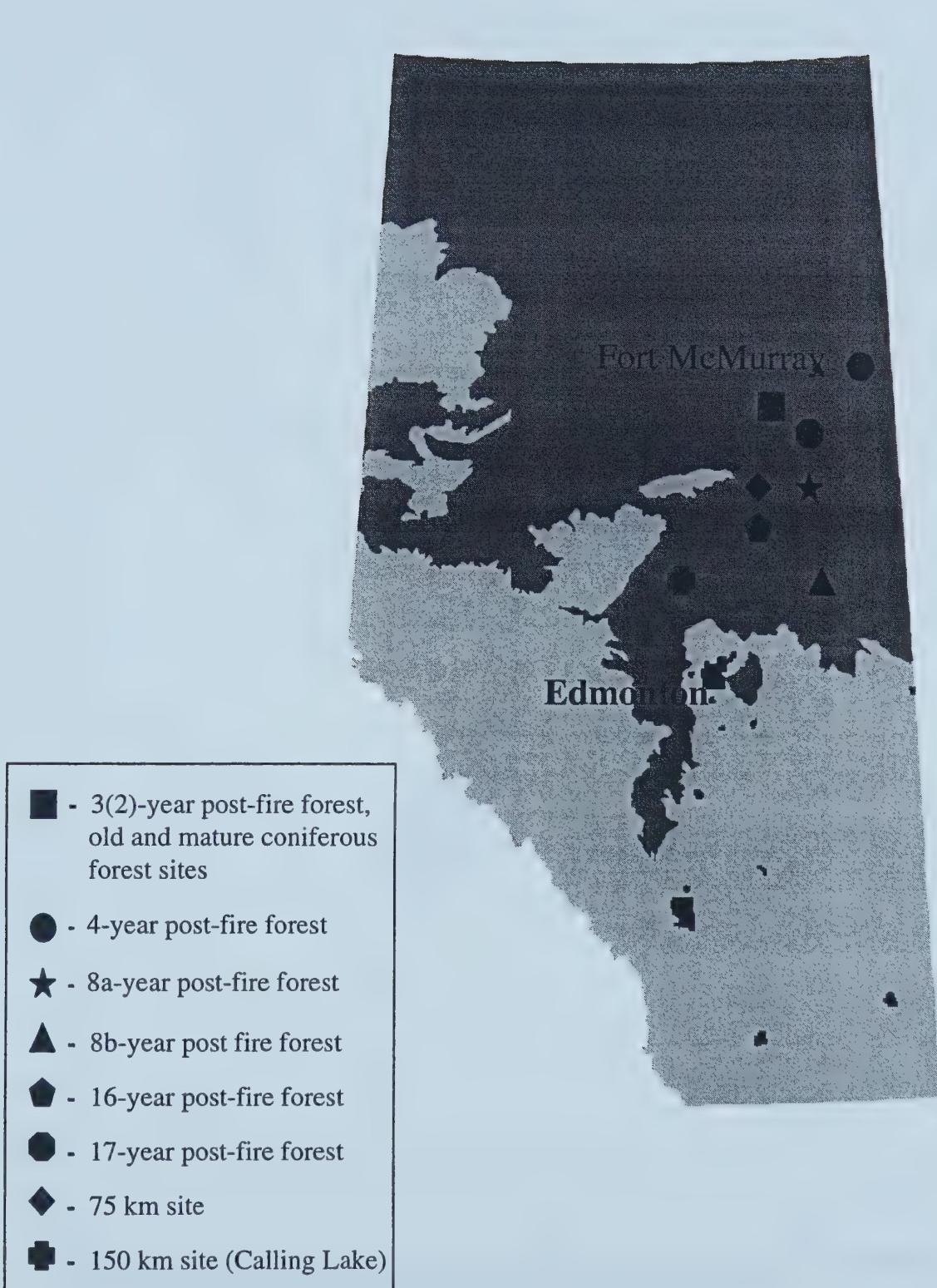
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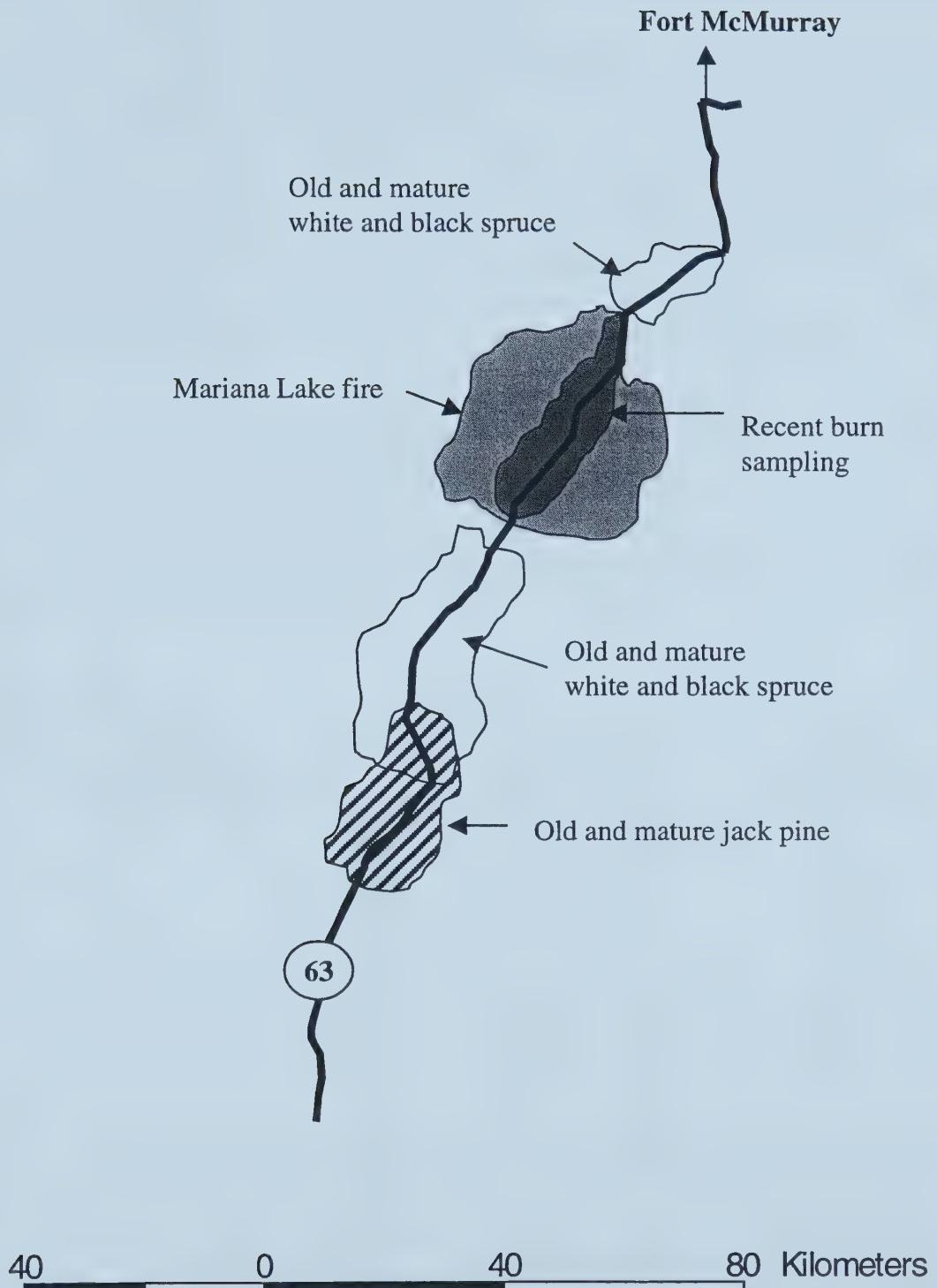
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APPENDICES



Appendix I. Location of study areas in the boreal forest of northeastern Alberta.
1 cm = approximately 100 km.



Appendix Chapter 2

Appendix 2.1. Location of 1997/1998 habitat association surveys

Appendix 2.2 Vegetation characteristics (mean + 95% confidence intervals) of unburned and recently burned sites occupied by Three-toed (TTWO) and Black-backed woodpeckers (BBWO). All vegetation characteristics except mean DBH (MDBH) represent density (# of trees / 100 m² of transects) at each site, and all variables were calculated using only those trees > 55 mm DBH. The number of sites represents the number of sites where woodpeckers were detected in a given habitat type. In unburned forests, vegetation characteristics of white and black spruce sites are based on birds detected at Mariana Lake, 75 km and 150 km sites. For recently burned forests I present data for white spruce sites, black spruce and jack pine sites combined and all three-habitat types combined. Since white spruce is commercially viable and salvage logged more often than black spruce and jack pine, I examined this habitat type separately for the purpose of management recommendations. I combined black spruce and jack pine sites since these two habitat types were where I conducted the majority of foraging observations. I used these sites to generate densities of standing dead trees and trees greater than 147 mm for the management recommendations since I did not examine tree densities during foraging observations. The variables outline under the Variables section are as follows: SW = white spruce, SB = black spruce, PJ = jack pine, DECID = deciduous, FB = balsam fir, RDT = recently dead trees, MDBH = mean DBH, STAND = density of standing trees, DOWN = density of downed trees, LBURN = lightly burned trees, MBURN = moderately burned trees, HBURN = heavily burned trees, DBH147 = trees greater than 147 mm DBH.

Unburned Forests

Habitat Type	# of Sites		Variables	TTWO	BBWO
	TTWO	BBWO		Mean + 95 CI	Mean + 95% CI
White spruce	13	1	SW	25.5 (16.6 – 34.4)	14.0
			SB	1.8 (0.3 – 3.4)	0.0
			FB	0.0	20.0
			PJ	2.0 (0 – 5.1)	0.0
			DECID	7.0 (4.2 – 9.8)	0.0
			RDT	4.7 (2.5 – 6.9)	8.0
			MDBH	246.3 (220 – 272)	261.8
			STAND	35.1 (30.4 – 39.7)	30.0
			DOWN	4.1 (1.7 – 6.5)	4.0
Black spruce	18	7	SB	55.0 (44.4 – 65.6)	53.6 (34.6 – 72.5)
			SW	1.1 (0 – 2.1)	4.6 (0 – 12.4)
			PJ	4.3 (1.6 – 7.1)	2.6 (0 – 6.7)
			DECID	2.4 (0.5 – 4.3)	3.0 (0 – 6.4)
			RDT	10.4 (6.7 – 14.2)	8.1 (1.5 – 14.8)
			MDBH	150.5 (135 – 166)	162.0 (115 – 209)
			STAND	52.5 (43.6 – 61.3)	60.3 (45.2 – 75.2)
			DOWN	10.8 (4.4 – 17.2)	7.4 (3.4 – 11.4)

Jack pine	2	0	PJ	24.7 (1.2 – 48.1)
			SB	21.3 (0 – 72.4)
			SW	4.0 (0 – 17.1)
			DECID	7.3 (0 – 22.3)
			RDT	3.0 (0 – 8.0)
			MDBH	176.5 (124 – 229)
			STAND	39.0 (16.9 – 61.1)
			DOWN	19.3 (0 – 64.4)

Recently Burned Forests

Habitat Type	# of Sites		Variables	TTWO	BBWO
	TTWO	BBWO		Mean + 95% CI	Mean + 95% CI
White spruce	6	9	SW	12.8 (9 – 16.7)	18.3 (6.1 – 30.6)
			SB	11.8 (4.3 – 19.3)	32.6 (5.8 – 16.0)
			PJ	1.3 (0 – 3.2)	7.1 (0 – 4.2)
			DECID	6.0 (0 – 14.2)	1.1 (0.3 – 10)
			LBURN	9.8 (0 – 25.6)	23.6 (0 – 16.3)
			MBURN	13.8 (4.6 – 23.1)	13.4 (6.5 – 28.4)
			HBURN	5.2 (1.8 – 8.5)	5.6 (4.0 – 14.0)
			MDBH	217.5 (174 – 261)	125.1 (180 – 258)
			DBH147	21.0 (9.7 – 32.3)	24.4 (13.1 – 35.8)
			STAND	28.5 (18.5 – 38.5)	31.3 (22.2 – 40.5)
Black spruce + Jack pine	7	15	DOWN	4.2 (0.5 – 8.2)	5.3 (0.3 – 10.4)
			SB	32.6 (16.2 – 48.9)	28.9 (16.4 – 41.4)
			PJ	7.1 (0 – 14.6)	11.9 (6.3 – 17.4)
			SW	5.7 (0.5 – 10.8)	4.1 (1.5 – 6.7)
			DECID	1.1 (0 – 2.7)	1.4 (0.1 – 2.8)
			LBURN	23.6 (10 – 37.2)	15.1 (7.3 – 22.9)
			MBURN	13.4 (6.0 – 20.8)	17.7 (12.5 – 23.0)
			HBURN	5.6 (0 – 11.4)	12.3 (5.9 – 18.6)
			MDBH	125.1 (104 – 146)	127.7 (116 – 140)
			DBH147	14.0 (5.6 – 22.3)	13.0 (9.3 – 16.7)
White spruce + Black spruce + Jack pine	13	24	STAND	40.0 (32.8 – 46.9)	38.1 (33.6 – 42.6)
			DOWN	7.7 (0 – 17.3)	9.3 (1.8 – 16.7)
			SW	9.0 (5.4 – 12.6)	9.5 (4.2 – 14.6)
			SB	23.0 (12.7 – 33.3)	22.1 (13.6 – 30.6)
			PJ	4.5 (0.5 – 8.4)	8.1 (4.1 – 12.1)
			DECID	3.4 (0 – 6.9)	2.8 (0.7 – 4.7)
White spruce + Black spruce + Jack pine	13	24	LBURN	17.2 (7.6 – 26.8)	11.9 (6 – 17.8)
			MBURN	13.6 (8.8 – 18.4)	17.6 (12.9 – 22.3)
			HBURN	5.4 (2.4 – 8.3)	11.0 (6.9 – 15.2)
			MDBH	167.7 (113 – 202)	161.8 (138 – 186)

DBH147	17.2 (11.1 – 23.3)	17.3 (12.4 – 22.2)
STAND	34.6 (28.5 – 40.7)	35.6 (31.4 – 39.8)
DOWN	6.1 (1.2 – 10.9)	7.8 (3.0 – 12.6)

Appendix: Chapter 3

Appendix 3.1. Black-backed woodpecker nesting data for nests located in the 3-year post-fire forest near Mariana Lake Alberta in 1997 and 1998. Nests 4 and 8 were reused in 1998. Burn classes of trees used for nesting are as follows: Burn class 1: 1-80% burn, bark intact; Burn class 2: 100% burn, 80-100% bark intact; and Burn class 3: 100% burn, 0-80% bark intact. Nest direction indicates the direction of the entrance hole.

Year	Nest #	Date Found/ Checked	Status	Previous Nest	DBH (mm)	Tree Species	Burn Class	Nest Height (m)	Nest Direction
1997	1	8 May	Excavating	No	255	Jack pine	2	6	SW
1997	2	8 May	Excavating	No	211	Jack pine	3	8	E
1997	3	31 May	Hatched	Unknown	290	Jack pine	1	8.5	S
1997	4	3 June	Hatched	Unknown	246	Black spruce	1	2	
1997	4	23 June	Fledged	Unknown	212	Jack pine	2	4.5	S
1998	4	6 May	Incubating	Unknown	210	Aspen	3	3.5	W
1998	4	13 May	Incubating	Unknown	271	Aspen	2	7	W
1998	4	20 May	Hatched	Unknown	198	Black spruce	2	1.25	E
1998	4	29 May	Hatched	Unknown	198	Black spruce	2	1.25	E
1997	5	3 June	Hatched	Unknown	212	Jack pine	2	4.5	S
1997	5	23 June	Fledged	Unknown	210	Aspen	3	3.5	W
1997	6	8 June	Hatched	Unknown	271	Aspen	2	7	W
1997	7	18 June	Hatched	Unknown	271	Aspen	2	7	W
1997	7	23 June	Fledged	Unknown	271	Aspen	2	7	W
1997	8	18 June	Hatched	Unknown	198	Black spruce	2	1.25	E

1997	8	23 June	Fledged					
1998	8	15 April	Laying	Yes				
1998	8	15 May	Hatched					
1998	8	26 May	Hatched					
1997	9	28 May	Hatched	Unknown	208	Black spruce	2	2.75
1998	10	6 May	Incubating	No	205	Jack pine	2	7.5
1998	10	13 May	Incubating					NE
1998	10	20 May	Hatched					
1998	11	9 May	Incubating	No	269	Jack pine	2	10
1998	11	15 May	Incubating					NE
1998	11	26 May	Hatch					
1998	12	8 May	Incubating	No	192	Black spruce	2	1.75
1998	12	20 May	Hatch					E
1998	12	21 May	Hatch					
1998	12	29 May	Hatch					
1998	12	30 May	Hatch					
1998	13	11 May	Hatch	No	255	Jack pine	2	Unknown
1998	13	31 May	Fledge					Unknown
1998	14	12 May	Incubating	No	211	White spruce	2	Unknown
1998	14	25 May	Hatch					Unknown
1998	15	13 May	Hatch	No	170	Jack pine	2	2.25
1998	15	24 May	Hatch					S
1998	15	25 May	Hatch					
1998	15	28 May	Hatch					

1998	16	16 May	Incubating	No	387	Aspen	3	3	NE
1998	16	23 May	Hatch						
1998	17	16 May	Incubating	No	268	Jack pine	2	6	SE
1998	17	23 May	Incubating						
1998	17	1 June	Hatch						
1998	18	19 May	Incubating	No	203	Aspen	3	2	S
1998	18	25 May	Hatch						
1998	18	1 June	Hatch						
1998	19	16 May	Hatch	No	256	Black spruce	2	3	SE
1998	20	17 May	Excavating	No	155	Black spruce	2	0.3	S
1998	20	30 May	Laying						
1998	21	18 May	Hatch	No	210	Black spruce	2	Unknown	Unknown
1998	21	22 May	Hatch						
1998	22	18 May	Incubating	No	173	Balsam	3	3.5	S
						poplar			

Appendix 3.2. A comparison of the dry weight of wood-boring insect larvae extracted from the roots of jack pine trees below the level of insect sampling and wood-boring larvae extracted from the basal sections of trees sampled in a 3-year post-fire forest. Wood-boring insect larvae were only detected in the basal sections of black spruce trees. Dry weights are reported in milligrams (mg).

Location of Extraction	Dry Weight (mg)
Basal section	91.5
Basal section	33.2
Basal section	58.8
Roots of jack pine	261.3
Roots of jack pine	201.1

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